RESOURCE PARTITIONING AMONG SYMPATRIC STELLER SEA LIONS AND NORTHERN FUR SEALS ON LOVUSHKI ISLAND, RUSSIA

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RESOURCE PARTITIONING AMONG SYMPATRIC STELLER SEA LIONS AND NORTHERN FUR SEALS ON LOVUSHKI ISLAND, RUSSIA

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Abstract

The competitive exclusion principle maintains that one of two non-interbreeding species occupying the same ecological niche and geographical territory will be displaced if population growth is not the same between species. Steller sea lions (*Eumetopias jubatus*; SSL) and northern fur seals (*Callorhinus ursinus*; NFS) breed sympatrically on four rookeries in the Russian Far East, creating the potential for inter-specific competition for limited prey resources. Approximately 1,000 SSL and 14,000 NFS breed on Lovushki Island in the Kuril Island chain. An additional 13,000–14,000 juvenile NFS are present during the breeding season.

The partitioning of forage resources among breeding SSL and both breeding and non-breeding NFS from 2003–2008 was examined through analysis of prey remains recovered from scats and spews, stable isotope (SI) analysis of vibrissae, fatty acid (FA) analysis of blubber, and analysis of foraging behavior through satellite-linked telemetry. Analysis of prey remains indicated a biologically significant overlap in the prey species and size selection of SSL and juvenile NFS and significant differences between the diets of SSL and breeding NFS. SSL fed primarily on Atka mackerel, while breeding NFS fed primarily on cephalopods and northern smoothtongue. SI analysis indicated significant differences in the trophic level and relative foraging location. SSL foraged at a higher trophic level, nearshore, and benthically, while NFS foraged at a lower trophic level, offshore, and pelagically. Analysis of FA signatures also suggested significant

differences in the relative diets of breeding NFS and SSL. Foraging behavior analysis also indicated that SSL foraged nearshore and benthically and breeding NFS foraged offshore and pelagically. The combination of these four methodologies suggests breeding NFS and SSL partition their forage resources by prey type and prey size, as well as spatially. This partitioning of resources between breeding animals currently allows both species to coexist within the same geographical region and likely reflected the differences in foraging abilities and provisioning strategies of the adults, as well as the fasting abilities of their pups. However, continued growth of the non-breeding NFS population on Lovushki Island may lead to the competitive exclusion of SSL due to inter-specific competition for food resources.

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GENERAL INTRODUCTION

The competitive exclusion principle originally postulated by Gause (1934) maintains that one of two non-interbreeding species occupying the same ecological niche and the same geographical territory will be displaced if population growth is not the same between species. Therefore, as population growth between natural populations is never identical, competition between sympatrically occurring species will result in the absolute exclusion of one of those species unless it is able to modify how it exploits the available resources (Hardin 1960). For most animals, the resource that is most often limiting is the available food base. To reduce inter-specific competition and minimize the risk of competitive exclusion or displacement, food resources may be partitioned based on the type or size of prey items consumed, or by spatially or temporally partitioning the foraging grounds.

Different methods of resource partitioning have been documented in a variety of animals. One of the most commonly documented means of dietary resource partitioning is by prey type. Zaret and Rand (1971) found that a decreased food supply during the dry season increases competition between nine species of sympatric freshwater fish in Panama, which results in a shift from widely overlapping diets during the wet season to specific, unique diets among the fish species during the dry season. Kitchen *et al.* (1999) found that swift foxes (*Vulpes velox*) and coyotes (*Canis latrans*) coexist in parts of Colorado due to partitioning of dietary resources based on prey type and size, where the foxes and coyotes prey primarily on smaller items such as rodents or on larger items such

as lagomorphs, respectively. Sympatrically occurring *Anolis* lizards on South Bimini Island also partition based on prey type, with some species foraging almost exclusively on ants while others supplement their diet with more fruit (Schoener 1968). Morphologically different insectivorous bats (Microchiroptera) in South Africa that forage in the same spatial locations have been shown to partition their prey items based on size (Aldridge and Rautenbach 1987), with larger bats taking larger specimens of beetles than smaller bats. Two species of sympatric mouse-eared bats (*Myotis* spp.) in Switzerland, nearly identical morphologically, were shown to partition their prey resources by specializing on grass- and ground-dwelling insects, respectively (Arlettaz 1999). Spatial partitioning of habitat has been found to occur in three species of sympatric orb-weaving spiders that spin their webs at different heights in the vegetation (Brown 1981) and by nine species of forest squirrels in Gabon that make use of different vertical layers of the rain forest vegetation (Emmons 1980). Temporal partitioning of foraging grounds has also been documented. Where spatial habitats overlap, Rocky Mountain elk (*Cervus elaphus nelsoni*) and Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) partition their available resources temporally through avoidance within a 7-day period (Stewart *et al.* 2002), thus reducing competitive interactions.

Dietary resource partitioning is also common among sympatrically occurring marine species. Partitioning based on prey type is common and has been documented to occur between cod (*Gadus morhua*) and minke whales (*Balaenoptera acustorostrata*) in the Barents Sea (Sivertsen *et al.* 2006), between bearded (*Erignathus barbatus*), ringed (*Phoca hispida*), ribbon (*Phoca fasciata*), and spotted (*Phoca largha*) seals in the Bering

Sea (Cooper *et al.* 2009), between New Zealand (*Arctocephalus forsteri*) and Australian (*Arctocephalus pusillus*) fur seals in southern Australia (Page *et al.* 2005), and many others. Sympatric ringed and ribbon seals in the Barents Sea partition their prey based on size (Wathne *et al.* 2000). Spatial partitioning of foraging grounds is also common in marine mammals. Sympatric Antarctic (*Arctocephalus gazella*) and Subantarctic (*Arctocephalus tropicalis*) fur seals in the Crozet Islands forage in distinctly different areas from one another (Bailleul *et al.* 2005). Humpback (*Balaenoptera musculus*) and minke whales in the Antarctic both feed on krill (*Euphausia superba*) but segregate their foraging locations based on depth and water temperature (Friedlaender *et al.* 2009). Similar resource partitioning strategies have also been documented in species such as southern elephant seals (*Mirounga leonina*) and New Zealand fur seals to reduce intra-specific competition among age, sex, and reproductive classes (Field *et al.* 2005, Page *et al.* 2005).

Competitive exclusion due to inter-specific competition has been shown to affect the geographic distribution of ecologically equivalent species of salamanders (Jaeger 1971), chipmunks (Brown 1971), foxes (Hersteinsson and Macdonald 1992), and mud snails (Race 1982, Brenchley and Carlton 1983), and the presence of domestic cattle results in the competitive displacement of Rocky Mountain elk in Colorado (Stewart *et al.* 2002). Competitive exclusion has been demonstrated between Risso's dolphins (*Grampus griseus*) and short-finned pilot whales (*Globicephala macrorhynchus*), two delphinid species of similar size with similar diets (Shane 1995). Bearzi (2005) suggests that distribution of bottlenose dolphins (*Tursiops truncates*), short-beaked common

dolphins (*Delphinus delphis*), and long-beaked common dolphins (*Delphinus capensis*) off the coast of Southern California is a consequence of inter-specific competition for prey that results in the competitive exclusion of two of these species from the specific habitat occupied by the other. Heithaus (2001) suggested that when prey resources are limited, inter-specific competition between sharks (order Selachii) and dolphins (suborder Odontoceti) with similar diets in South Africa leads to niche divergence.

Steller sea lions (SSL, *Eumetopias jubatus*) breed sympatrically with northern fur seals (NFS, *Callorhinus ursinus*) on four rookeries in the Russian Far East: Medny Island (54.8667° N, 167.3667° E) in the Commander Island group, Srednego (47.5797° N, 152.9083° E) and Lovushki (48.5436° N, 153.6736° E) Islands in the Kuril Island chain, and Tuleny Island (48.5° N, 144.6334° E) in the western Sea of Okhotsk (Figure 1). Approximately 46% of the total SSL breeding population and approximately 43% of the total SSL pup production in Russian waters occurs on these rookeries (Burkanov and Loughlin 2005). Ship-based surveys conducted between 2002 and 2005 estimated a range-wide SSL population of 62,000–74,000 animals (Burkanov and Loughlin 2005, Pitcher *et al.* 2007) with approximately 16,000 (22–25%) located along the coastal waters of Russia and northern Japan (Burkanov and Loughlin 2005). As in North American waters, the Asian subpopulation of SSL experienced a dramatic decline and has been unstable for the past 4 decades (Loughlin *et al.* 1992, Burkanov and Loughlin 2005). In 1994, the SSL was listed as an endangered species in the Russian Red Book. On Lovushki Island, the abundance of non-pup SSL dropped from approximately 4,000 in 1955 to approximately 760 by 1989 (Burkanov and Loughlin 2005). After a slight

Figure 1. Photographs of sympatric northern fur seals (dark brown) and Steller sea lions (light brown) on Lovushki Island in 2008 (upper panel) and Tuleny Island in 2004 (lower panel).

increase, the population has remained at an average of 1,039 SSL from 1995 through 2005 (Burkanov and Loughlin 2005).

Prior to being eradicated due to unregulated harvesting in the late 19th century, the non-pup population of NFS in the Kuril Islands was estimated to have been at least 15,000 (Snow 1897). A slow re-establishment of breeding colonies occurred in the early 20th century, and surveys conducted in 1955–56 counted approximately 2,000 fur seals on Lovushki Island and an additional 800–900 on Srednego Island (Klumov 1957). The non-pup population in this region continued to grow at 19.9% per year until 1978 and then remained relatively stable at an average of 8,063 for the next decade (Kuzin 1999). A rapid increase in NFS population numbers ensued during the early 21st century with pup counts on Lovushki Island increasing to approximately 12,180 pups by 2006 (Burkanov *et al.* 2007). Using a method of estimating total abundance wherein pups are considered to be an average of 30% of the total population (Kuzin 1999), the total non-pup NFS population in 2006 on Lovushki Island alone was estimated at 28,420.

SSL and NFS are both piscivorous, sexually dimorphic pinnipeds with similar ecological requirements and life history traits. The mass of adult male SSL is up to 1,120 kg and females to 350 kg (Loughlin *et al.* 1987) while the mass of adult male NFS is up to 320 kg and females to 71 kg (Scheffer and Wilke 1953). The foraging behavior of NFS and SSL is similar, with variations resulting from differences in prey availability, season, and local bathymetric and oceanographic conditions. NFS and SSL have similar diets, typically consuming species such as walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*), salmon (*Oncorhynchus* spp.), cephalopods,

and a variety of forage fish such as capelin (*Mallotus villosus*), herring (*Clupea pallasi*), and northern smoothtongue (*Leuroglossus schmidti*) (Sinclair *et al.* 1994, Merrick *et al.* 1997, Waite and Burkanov 2006, Zeppelin and Ream 2006, McKenzie and Wynne 2008). SSL typically forage at depths <30 m during the evening, night, and early morning hours but are known to forage at >250 m, especially during the day (Merrick *et al.* 1994, Merrick and Loughlin 1997, Loughlin *et al.* 1998). Pelagically foraging NFS also typically dive to depths <30 m during the night, but NFS that feed either benthically or on non-vertically migrating prey will dive to depths >75 m throughout the day (Gentry *et al.* 1986a). With overlapping breeding periods (May–August) the adults of both species become highly territorial and males vigorously defend harems of breeding females, and with a 2–3 month overlap in pup nursing, foraging also becomes competitive because adult females of both species are central place foragers, alternating between periods of foraging at sea and nursing their pups on land (Mathisen *et al.* 1962, Pitcher and Calkins 1981, Gentry and Kooyman 1986, Gentry 2002).

Kuzin *et al.* (1977) hypothesized that NFS competitively displace SSL on Kuril Island rookeries during periods of increased NFS population size and Loughlin and Miller (1989) suggested the potential for a similar response on Bogoslof Island, Alaska. Therefore, the goal of this project was to examine the resource partitioning among sympatrically occurring SSL and NFS on Lovushki Island, Russia (Figure 2), in order to assess the potential for the competitive exclusion of SSL during a period when the rapidly expanding NFS population has reached a historic high. To accurately assess the level of

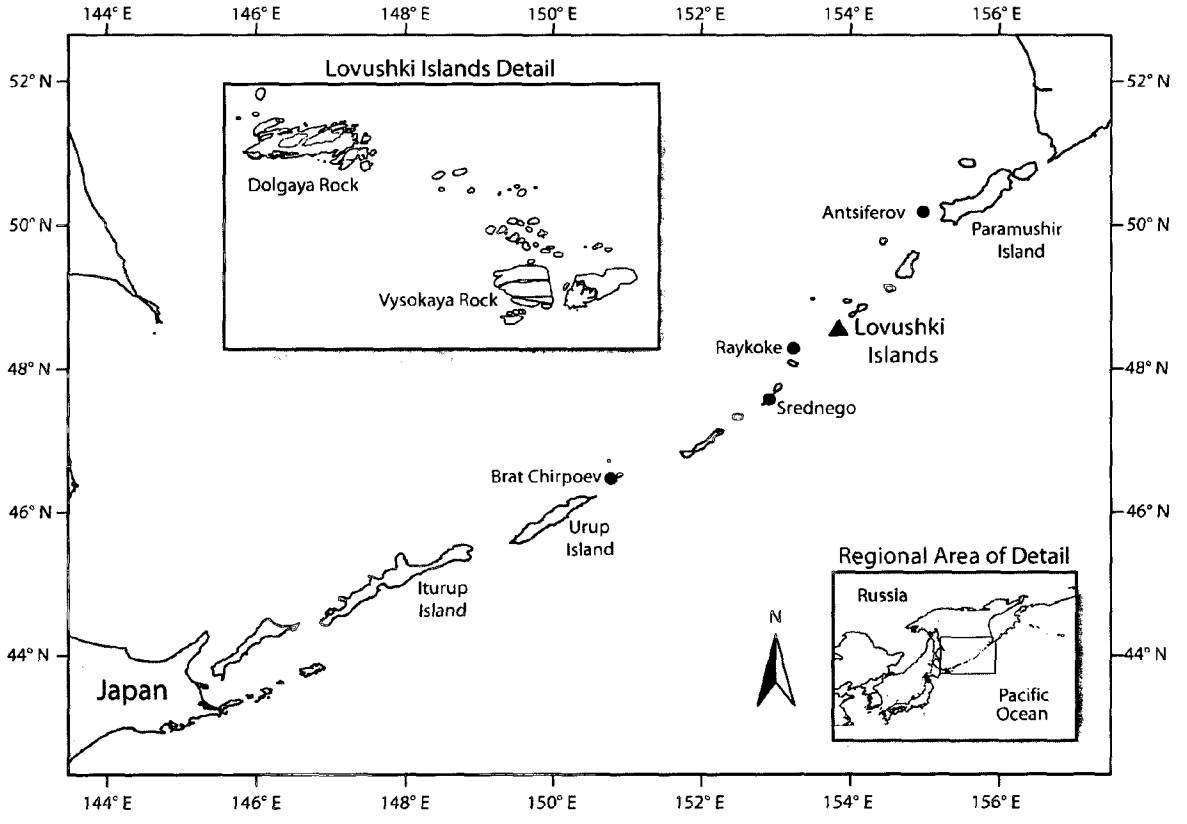

Figure 2. Location of the Lovushki Islands study site (filled triangle).

dietary overlap and potential for inter-specific competition, four different techniques were used to estimate the diet composition and foraging locations of both predator species at different temporal scales. In Chapter 1, the diet composition of breeding female SSL, breeding female NFS, and non-breeding juvenile NFS is estimated through the analysis and identification of undigested prey remains recovered from scats and spews collected on Lovushki Island during the breeding seasons of 2003, 2005, 2007, and 2008. Differences in the prey species, minimum number of individual prey items consumed, and the relative sizes of the prey items consumed are examined. Genetic analyses were performed on samples collected from portions of the rookery where substantial mixing of species occurs to determine the species of origin. The analysis of samples from a single collection effort provides information on prey consumed during the animal's most recent meal. Multiple collections were made during each breeding season so that an estimate of diet composition representative of the entire breeding season could be made.

In Chapter 2, resource partitioning based on prey type and foraging location is examined through biochemical analyses of samples collected in 2007 and 2008. Ratios of stable carbon and nitrogen isotopes in the roots of vibrissae collected from adult female SSL and NFS and their pups are used to estimate trophic level and relative foraging location and reflect the diet integrated over the previous 2 weeks. Differences in dietary composition are also examined through the analysis of fatty acid profiles of blubber collected from both predator species. These samples represent the diet integrated over the previous 30 days. While specific prey items could not be determined using either of these two methods, general dietary differences could be inferred.

The spatial partitioning of the foraging grounds is examined through the use of time-depth recorders and satellite telemetry in Chapter 3. The movements and diving behavior of adult female NFS and SSL were monitored over a period of 4–44 days in 2007 and 2008. Differences in dive depth and duration, foraging trip distance and duration, and the location of foraging bouts were examined and the results are compared to the diet composition and foraging location estimates inferred from the analysis of scats and spews, vibrissal roots, and blubber.

This study is the first to examine the resource partitioning of two sympatrically occurring animals through the simultaneous use of all four of these methodologies. This is also the first study which applies molecular techniques to examine dietary differences between sympatrically occurring SSL and NFS.

CHAPTER 1. ANALYSIS OF SCATS AND SPEWS

INTRODUCTION

Historic data on the diet of SSL and NFS in Russian waters are sparse. Based on analyses of stomach contents, the diets of NFS and SSL on their allopatric sites in the Kuril Islands were similar in the 1950s and 60s (Panina 1964, Belkin 1966, Panina 1966, Kuzin *et al.* 1977) with walleye pollock (*Theragra chalcogramma*) accounting for the majority of the NFS and SSL diet. Rockfish (*Sebastodes* sp.), Okhotsk Atka mackerel (*Pleurogrammus azonus*), sandlance (*Ammodytes* hexapterus), and cephalopods were also predominant (Belkin 1966). Kuzin *et al.* (1977) described a partitioning of diet between the two pinniped species in the early 1970's on sympatric rookeries in the Kuril Islands: the frequency of occurrence of prey remains recovered from stomachs of NFS was 75.8% Commander squid (*Berryteuthis magister*), 27.6% Japanese flying squid (*Todarodes pacificus*), and 3.4% pollock, while stomachs of SSL contained 70.7% pollock, 26.8% Octopoda, 31.7% Commander squid, 12.1% Japanese flying squid, and 7.3% Hexagrammidae. During this period, the population of NFS was relatively low and outnumbered SSL at less than 2.5:1 (Kuzin *et al.* 1977), compared with the 28:1 ratio in 2006.

The North Pacific and Bering Sea experienced oceanographic regime shifts in 1976–1977 and 1989 that resulted in marked changes in the abundance and distribution of the primary prey of both SSL and NFS (Anderson and Piatt 1999, Benson and Trites

2002, Conners *et al.* 2002). There are no data to suggest that the changes experienced in the North Pacific and Bering Sea affected the prey abundance and distribution in Russian waters. Waite and Burkanov (2006) presented the most recent data on SSL prey selection on allopatric sites throughout the majority of their Russian range and suggested that while pollock had been one of the major prey items, it had been replaced by salmon and Atka mackerel (*Pleurogrammus monopterygius*) as the dominant prey items of SSL on rookeries in the Kuril Islands.

Recent studies on NFS diet in Russian waters are extremely limited; however, data from other regions of the northern Pacific Ocean indicate some dietary overlap between the two species. Stomachs from juvenile and adult NFS captured off the Pacific coast of northern Japan in 1997–98 contained primarily squid, smelt, anchovy, headlightfish (*Diaphus* sp.), and lampfish (Myctophidae) (Yonezaki *et al.* 2003). Prey items found in SSL scats collected on haul-outs in the southern Kuril Islands near Japan were similar, consisting of large numbers of anchovy, gadids, and squid (Waite and Burkanov 2006). Walleye pollock and Atka mackerel were important prey items for both NFS and SSL in the Aleutian and Pribilof Islands from 1981–2005 (Sinclair *et al.* 1994, Merrick *et al.* 1997, Zeppelin and Ream 2006, McKenzie and Wynne 2008).

Antonelis *et al.* (1997) found that NFS on Medny Island in 1988 consumed primarily squid and relatively little Atka mackerel while Waite and Burkanov (2006) found that SSL on Medny Island in 2001 consumed exclusively Atka mackerel ($n = 12$). There are no known published studies containing recent data on SSL or NFS diets on the remaining three sympatric rookeries, primarily due to difficulties in distinguishing

between the scats of the two species. Therefore, very little is known regarding prey selection trends, diet diversity, or level of competition for prey resources with commercial fisheries over the last several decades for a substantial portion of the SSL and NFS population. Similar life history traits and ecological requirements, along with recent growth in the local population of both species, increase the potential for elevated inter-specific competition for food resources. This study combines the identification of predator scat using fecal DNA and the analysis of undigested prey remains to examine the use of prey resources by SSL and NFS on Lovushki Island, one of four rookeries in the Russian Far East where these two species breed sympatrically (Figure 2).

METHODS

Sample collection and processing

During the breeding seasons of 2003, 2005, 2007, and 2008 (June through August) we collected a total of 495 scats and 44 spews from both the breeding and non-breeding portions of the rookery at Lovushki Island. We obtained an additional six fecal samples via enema (Yonezaki *et al.* 2004), five fecal samples via normal defecation, and two stomach content samples via gastric lavage (Antonelis *et al.* 1987) from breeding female fur seals while they were restrained during concurrent research projects.

Scat and spew samples were collected opportunistically when the rookery was disturbed for concurrent research projects. On the most densely populated portions of the

rookery breeding SSL segregate into groups, which were usually surrounded by groups of breeding NFS. These areas were visually monitored by field observers present on the rookery for the duration of the breeding season. Only fresh scats were collected in these areas to maximize the likelihood that we could positively identify which species had deposited the fecal samples. Because the boundaries of these groups are plastic, scats collected near the edges were sub-sampled for genetic analysis and species verification (n = 51). In locations where significant species mixing occurs, each scat was sub-sampled for genetic analysis before removal from the substrate (n = 63). Samples collected in these areas were considered to be primarily from breeding animals. The remainder of the samples collected from non-breeding portions of the rookery and outlying rocks inhabited exclusively by NFS were considered to be from non-breeding NFS.

The genetic sub-samples were collected and stored according to Murphy *et al.* (2002) wherein 1–2 ml of fecal material per scat was collected, placed in 95% ethanol at a 4:1 (ethanol:feces) ratio by volume, and stored either at room temperature or at -80°C. Fecal genetic samples were analyzed at the University of Idaho (Moscow, Idaho) according to Waite *et al.* (In press) to determine the species of origin.

Each scat was placed in a separate plastic bag and processed onboard a support vessel. The plastic bags were filled with water and a mild detergent and allowed to soak for 24–48 hours while being agitated by the movement of the vessel. The resulting slurry was rinsed through a series of three nested mesh sieves (1.000 mm, 0.710 mm, and 0.500 mm). Solid fecal material was gently manipulated with a soft brush and rinsed with water until it passed through the sieves (Treacy and Crawford 1981).

Prey species were enumerated and identified to the lowest possible taxonomic group by Pacific Identifications, Inc. (Victoria, British Columbia) from the dried hard parts. All identifiable skeletal structures (versus only otoliths) were used to reduce the problems associated with differential digestion of smaller or more delicate prey items (Browne *et al.* 2002, Tollit *et al.* 2006). The minimum number of individuals (MNI) consumed for each prey type was estimated by counting a variety of key diagnostic structures. Prey size was estimated and grouped into species-specific size categories based on an extensive reference collection of skeletal remains.

Statistical analysis

For general diet descriptions, data from scats and spews were pooled to accurately assess frequency of occurrence, prey size, and total number of prey. Pooling scat and spew data also reduces the biases associated with analyzing scat or spew separately (Page *et al.* 2005, Gudmundson *et al.* 2006), as spews often contain prey remains too large to pass through the pyloric sphincter and increased numbers of cephalopod beaks that had accumulated in the folds of the stomach lining (Jobling and Breiby 1986, Harvey and Antonelis 1994). For comparisons between scats and spews, enema samples were grouped with scats and stomach samples were grouped with spews. The relative importance of each prey type was calculated using (1) simple frequency of occurrence (FO_i):

$$FO_i = \left(\frac{n_i}{n_t}\right) \times 100 \quad (1)$$

where n_i is the number of samples containing prey type i and n_t is the total number of samples examined; and (2) percent numerical abundance (NA_i), a measure of dominance:

$$NA_i = \left(\frac{MNI_i}{MNI_t}\right) \times 100 \quad (2)$$

where MNI_i is the minimum number of individuals of prey type i consumed and MNI_t is the minimum number of all prey items consumed. NA_i was calculated for spew and scat samples combined and for scat samples only (NA_i^S). An adjusted MNI_i (MNI_i^*) was calculated for each prey type by applying numerical correction factors (NCF) published for Steller sea lions (Tollit *et al.* 2007) to scat samples to account for species-specific differences in complete prey digestion. Adjusted NA_i values (NA_i^*) and 95% confidence intervals were computed. Size-specific NCFs were applied when available (Tollit et al. 2007). There are currently no published prey-specific correction factors available for NFS.

Binary logistic regression models were used to determine if the occurrence of prey varied by predator species, reproductive group, or sample type. The presence or absence of each prey type was modeled as a binary response variable with species-reproductive group (SSL breeding, NFS breeding, and NFS non-breeding), sample type (scat or spew), and the interaction between group and sample type as explanatory variables. If a significant interaction term was added to the model, sample types within each group were compared.

Fligner–Policello tests were performed to test for differences in number of prey species and MNI_i found in individual samples between scats and spews, predator species, and reproductive groups. The Fligner–Policello statistic tests for differences in central tendency among samples with unequal variances and was selected due to its robustness concerning violations of the assumption of symmetrical distributions (Fligner and Policello II 1981).

To quantify the dietary overlap among reproductive and species groups, we calculated Pianka's niche overlap index (O_{jk}) (Pianka 1973):

$$O_{jk} = \frac{\sum_{i=1}^{m}\left(p_{ij} \times p_{ik}\right)}{\sqrt{\sum_{i=1}^{m} p_{ij}^2 \times \sum_{i=1}^{m} p_{ik}^2}} \tag{3}$$

where p_{ij} and p_{ik} are the percent numerical abundance (NA) of the ith prey type for the predator groups j and k being compared. The index O_{jk} ranges from 0 to 1 where 0 indicates no dietary resource sharing between the two groups and 1 indicates a complete overlap in their diet. A value greater than 0.6 is considered to be a "biologically significant" overlap (Zaret and Rand 1971, Mathur 1977, Wallace 1981). The niche overlap index for each pair of groups was calculated based on NA_i, NA_i^s, and NA_i^*. Pearson's chi-square contingency table analyses were performed to test for differences in the size of prey items consumed between predator groups with a biologically significant niche overlap index. When a contingency table contained a cell size of <5, p-values were computed for a Monte Carlo test using 1000 replicates (Hope 1968). Contingency table tests were only performed for prey species that occurred in ≥5% of scats.

The diversity of the diet of each species and reproductive group was calculated using Shannon's index of diversity:

$$H = -\sum_{i=1}^{k} p_i \ln p_i \quad (5)$$

where p_i is the numerical abundance of the ith prey type (NA_i), and k is the number of prey types.

Associations between prey types found in individual samples were examined by calculating Pearson partial correlation coefficients for each pair of prey types within each predator species and reproductive group. Partial correlation takes into account the interactions of other prey types on the two species under consideration. Correlations between prey species were illustrated with a dendrogram produced through an agglomerative hierarchical cluster analysis. Clustering method was set to "average" and the distance between prey types was set to 1 minus the Pearson partial correlation coefficient of those two items (McGarigal *et al.* 2000).

Unless otherwise noted, all statistical analyses and calculation of indices were performed using five prey groups, which consisted of species that occurred in ≥5% of all samples: Atka mackerel, salmon, walleye pollock, cephalopods, and northern smoothtongue. Scats that were without hard parts or remains that could not be identified to at least family level were not included in the analyses. Sample size was considered to be insufficient to test for differences between years based on analyses by Trites and Joy (2005). Simple bootstrapping was used to estimate 95% confidence intervals (CI) around the overlap and diversity indices. Differences between the bootstrapped confidence

intervals were calculated to test for differences in indices among groups. All means are reported ±SEM. Statistical analyses were performed using R version 2.9.2 (The R Foundation for Statistical Computing) and SAS version 9.1 (SAS Institute Inc, Cary, North Carolina).

RESULTS

Genetic analysis

Of the 114 fecal subsamples genetically analyzed to determine species, 28 were determined to be from fur seals and 78 from sea lions. A total of 10 samples could not be identified to species due to problematic DNA extractions or amplification failure, and were not included in the analyses. Of the 51 scat samples that were collected near the boundary between groups of SSL and NFS, approximately 12% ($n = 6$) had been incorrectly identified in the field based on collection location but correctly identified using molecular techniques, emphasizing the importance of genetic testing.

Fur seal diet

Of the 242 scats and 45 spews collected from NFS, 198 scats (81.8%) and 43 spews (95.5%) contained prey remains that could be minimally identified to the family level. No prey remains were found in 13 (5.4%) of the scats. The remaining scats (12.8%) and spews (4.5%) contained unidentifiable prey remains. A total of 21 different prey types were identified with nine identified to species. Overall, the most common prey items, in order of frequency of occurrence, were Atka mackerel (50.0%), salmon (37.6%), cephalopods (28.5%; primarily *Gonatopsis* sp. cf. *G. borealis*), walleye pollock (26.3%), and northern smoothtongue (17.5%). The most dominant prey items, in order of numerical abundance, were cephalopods (27%), northern smoothtongue (25.8%), Atka mackerel (19.2%), walleye pollock (12.6%), and salmon (8.7%) (Figure 3, Table 1).

Diet composition varied between reproductive groups; salmon (*FO* = 43.4%), cephalopods (*FO* = 41.4%), and Atka mackerel (*FO* = 31.7%) were the most frequently occurring taxa in the breeding NFS diet; however, northern smoothtongue (*NA* = 40.9%) and cephalopods (*NA* = 31.5%) were the most numerically abundant (Table 2). The most frequently occurring taxa in the non-breeding NFS diet (Table 3) were Atka mackerel (*FO* = 69.1%), pollock (*FO* = 36.0%), and salmon (*FO* = 31.6%); however, cephalopods (*NA* = 23%) were more numerically abundant than salmon (*NA* = 7.9%). Based on frequency of occurrence, breeding NFS consumed significantly more cephalopods (χ^2 = 29.76, $p < 0.001$), northern smoothtongue ($\chi^2 = 20.41$, $p < 0.001$), and salmon ($\chi^2 = 6.70$, $p = 0.010$) than non-breeding NFS. Non-breeding NFS consumed

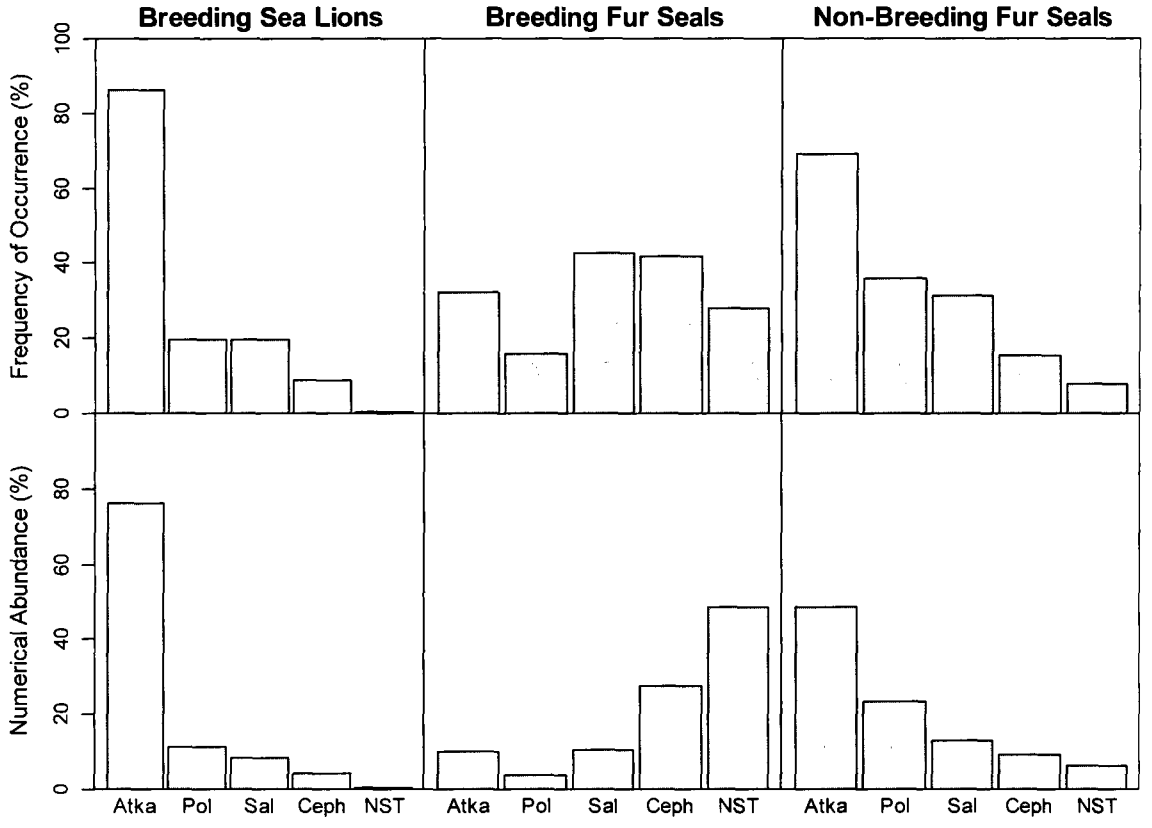

Figure 3. Frequency of occurrence and dominance of prey items found in scats and spews of Steller sea lions and northern fur seals collected from Lovushki Island, Russia, during the breeding seasons of 2003, 2005, 2007, and 2008. Atka = Atka mackerel, Pol = Walleye pollock, Sal = Salmon, Ceph = Cephalopods, NST = northern smoothtongue.

Table 1. Minimum number of individual prey items consumed (MNI), percent numerical abundance (NA), and percent frequency of occurrence (FO) of prey taxa found in scats and spews from total (breeding and non-breeding) northern fur seals collected on Lovushki Island during the breeding seasons of 2003, 2005, 2007, and 2008. The total number of samples collected and the total number of samples with prey remains are in parentheses. Grouped totals are in bold.

	2003 (n = 42/35)			2005 (n = 48/48)			2007 (n = 105/98)			2008 (n = 93/93)			Total (n = 288/274)		
Prey Type	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**
Fish	**112**	**85.5**	**97.1**	**220**	**71.4**	**95.8**	**254**	**89.4**	**98.0**	**330**	**66.9**	**93.5**	**916**	**73.0**	**96.0**
Unidentified fish	6	4.6	17.1	5	1.6	10.4	23	8.1	23.5	15	3.0	16.1	49	3.9	17.9
Hexagrammidae	**34**	**26.0**	**57.1**	**37**	**12.0**	**37.5**	**82**	**28.9**	**52.0**	**89**	**18.1**	**51.6**	**242**	**19.3**	**50.0**
Atka mackerel	34	26.0	57.1	37	12.0	37.5	82	28.9	52.0	88	17.8	51.6	241	19.2	50.0
Rock greenling										1	0.2	1.1	1	0.1	0.4
Gadidae	**2**	**1.5**	**5.7**	**1**	**0.3**	**2.1**	**40**	**14.1**	**28.6**	**118**	**23.9**	**46.2**	**161**	**12.8**	**27.0**
Unidentified gadid				1	0.3	2.1				1	0.2	1.1	2	0.2	0.7
Walleye pollock	2	1.5	5.7				40	14.1	28.6	116	23.5	45.2	158	12.6	26.3
Pacific cod										1	0.2	1.1	1	0.1	0.4
Salmon	18	13.7	48.6	37	12.0	75.0	26	9.2	25.5	28	5.7	26.9	109	8.7	37.6
N. smoothtongue	26	19.8	17.1	140	45.5	39.6	81	28.5	7.1	77	15.6	17.2	324	25.8	17.5
Other fish species	**26**	**19.8**	**34.3**				**2**	**0.7**	**2.0**	**3**	**0.6**	**2.2**	**31**	**2.5**	**5.8**
Sculpin	12	9.2	14.3										12	1.0	1.8
Irish lord	1	0.8	2.9										1	0.1	0.4
Herring	1	0.8	2.9										1	0.1	0.4
Lampfish							1	0.4	1.0				1	0.1	0.4
High cockscomb							1	0.4	1.0	1	0.2	1.1	2	0.2	0.7
Prickleback										2	0.4	1.1	2	0.2	0.4
Sand lance	2	1.5	2.9										2	0.2	0.4
Snailfish	2	1.5	2.9										2	0.2	0.4
Stone cockscomb	8	6.1	22.9										8	0.6	2.9
Cephalopods	**19**	**14.5**	**25.7**	**88**	**28.6**	**41.7**	**30**	**10.6**	**14.3**	**201**	**40.8**	**37.6**	**338**	**27.0**	**28.5**
Unidentified ceph.	1	0.8	2.9	46	14.9	20.8	6	2.1	5.1	40	8.1	14.0	93	7.4	10.6
Squid	18	13.7	22.9	42	13.6	37.5	24	8.5	11.2	160	32.5	30.1	244	19.5	23.7
Octopus										1	0.2	1.1	1	0.1	0.4
Other Prey*	**2**		**5.7**	**83**		**33.3**	**3**		**3.1**	**11**		**9.7**	**99**		**10.9**
Bird	1		2.9										1		0.4
Polychaete worm	1		2.9	83		33.3	3		3.1	11		9.7	98		10.6

* Polychaete worms and birds were considered to be secondary or incidental prey items and therefore not included in the calculations of percent numerical abundance.

Table 2. Minimum number of individual prey items consumed (MNI), percent numerical abundance (NA), and percent frequency of occurrence (FO) of prey taxa found in scats and spews from breeding northern fur seals collected on Lovushki Island during the breeding seasons of 2003, 2005, 2007, and 2008. The total number of samples collected and the total number of samples with prey remains are in parentheses. Grouped totals are in bold.

	2003 (n = 12/11)			2005 (n = 36/36)			2007 (n = 48/46)			2008 (n = 51/51)			Total (n = 148/145)		
Prey Type	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**
Fish	**46**	**71.9**	**90.9**	**167**	**69.6**	**100.0**	**140**	**83.8**	**95.7**	**144**	**57.8**	**88.5**	**497**	**65.6**	**93.8**
Unidentified fish	2	3.1	18.2	5	2.1	13.9	15	9.0	32.6	12	4.8	21.2	34	4.5	22.8
Hexagrammidae	**2**	**3.1**	**18.2**	**5**	**2.1**	**13.9**	**26**	**15.6**	**41.3**	**31**	**12.4**	**38.5**	**64**	**8.4**	**31.7**
Atka mackerel	2	3.1	18.2	5	2.1	13.9	26	15.6	41.3	30	12.0	38.5	63	8.3	31.7
Rock greenling		0.0								1	0.4	1.9	1	0.1	0.7
Gadidae	**1**	**1.6**	**9.1**				**4**	**2.4**	**8.7**	**27**	**10.8**	**36.5**	**32**	**4.2**	**16.6**
Unidentified gadid		0.0						0.0		1	0.4	1.9	1	0.1	0.7
Walleye pollock	1	1.6	9.1				4	2.4	8.7	26	10.4	34.6	31	4.1	15.9
Salmon	**7**	10.9	63.6	29	12.1	77.8	14	8.4	30.4	17	6.8	26.9	67	8.8	43.4
N. smoothtongue	25	39.1	45.5	128	53.3	36.1	80	47.9	13.0	77	30.9	30.8	310	40.9	27.6
Other fish species	**9**	**14.1**	**36.4**				**1**	**0.6**	**2.2**	**1**	**0.4**	**1.9**	**11**	**1.5**	**4.1**
High cockscomb		0.0					1	0.6	2.2				1	0.1	0.7
Irish lord	1	1.6	9.1										1	0.1	0.7
Prickleback		0.0								2	0.8	1.9	2	0.3	0.7
Sculpin	2	3.1	18.2										2	0.3	1.4
Snailfish	2	3.1	18.2										2	0.3	1.4
Stone cockscomb	4	6.3	36.4										4	0.5	2.8
Cephalopods	**18**	**28.1**	**72.7**	**73**	**30.4**	**36.1**	**27**	**16.2**	**26.1**	**121**	**48.6**	**51.9**	**239**	**31.5**	**41.4**
Unidentified ceph.	1	1.6	9.1	41	17.1	22.2	3	1.8	6.5	35	14.1	19.2	80	10.6	15.2
Squid	17	26.6	63.6	32	13.3	33.3	24	14.4	23.9	86	34.5	42.3	159	21.0	35.9
Other Prey*	**2**		**18.2**	**55**		**33.3**	**2**		**4.3**	**11**		**17.3**	**70**		**17.2**
Bird	1		9.1										1		0.7
Polychaete worm	1		9.1	55		33.3	2		4.3	11		17.3	69		16.6

* Polychaete worms and birds were considered to be secondary or incidental prey items and therefore not included in the calculations of percent numerical abundance.

Table 3. Minimum number of individual prey items consumed (MNI), percent numerical abundance (NA), and percent frequency of occurrence (FO) of prey taxa found in scats and spews from non-breeding northern fur seals collected on Lovushki Island during the breeding seasons of 2003, 2005, 2007, and 2008. The total number of samples collected and the total number of samples with prey remains are in parentheses. Grouped totals are in bold.

	2003 (n = 25/31)			2005 (n = 16/16)			2007 (n = 56/52)			2008 (n = 43/43)			Total (n = 157/136)		
Prey Type	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**
Fish	**66**	**98.5**	**100.0**	**95**	**66.9**	**100.0**	**114**	**97.4**	**100.0**	**164**	**67.2**	**97.7**	**439**	**77.0**	**99.3**
Unidentified fish	4	6.0	16.0	1	0.7	6.3	8	6.8	15.4	3	1.2	7.0	16	2.8	11.8
Hexagrammidae	**32**	**47.8**	**72.0**	**35**	**24.6**	**100.0**	**56**	**47.9**	**61.5**	**58**	**23.8**	**65.1**	**181**	**31.8**	**69.1**
Atka mackerel	32	47.8	72.0	35	24.6	100.0	56	47.9	61.5	58	23.8	65.1	181	31.8	69.1
Gadidae	**1**	**1.5**	**4.0**	**1**	**0.7**	**6.3**	**36**	**30.8**	**46.2**	**90**	**36.9**	**55.8**	**128**	**22.5**	**36.8**
Unidentified gadid				1	0.7	6.3							1	0.2	0.7
Walleye pollock	1	1.5	4.0				36	30.8	46.2	90	36.9	55.8	127	22.3	36.0
Pacific cod										1	0.4	2.3	1	0.2	0.7
Salmon	11	16.4	40.0	11	7.7	68.8	12	10.3	21.2	11	4.5	25.6	45	7.9	31.6
N. smoothtongue	1	1.5	4.0	47	33.1	56.3	1	0.9	1.9				49	8.6	8.1
Other fish species	**17**	**25.4**	**32.0**				**1**	**0.9**	**1.9**	**1**	**0.4**	**2.3**	**19**	**3.3**	**7.4**
Sculpin	10	14.9	12.0										10	1.8	2.2
Herring	1	1.5	4.0										1	0.2	0.7
Lampfish							1	0.9	1.9				1	0.2	0.7
High cockscomb										1	0.4	2.3	1	0.2	0.7
Sand lance	2	3.0	4.0										2	0.4	0.7
Stone cockscomb	4	6.0	16.0										4	0.7	2.9
Cephalopods	**1**	**1.5**	**4.0**	**47**	**33.1**	**62.5**	**3**	**2.6**	**3.8**	**80**	**32.8**	**18.6**	**131**	**23.0**	**15.4**
Unidentified ceph.				23	16.2	25.0	3	2.6	3.8	5	2.0	7.0	31	5.4	6.6
Squid	1	1.5	4.0	24	16.9	56.3				74	30.3	11.6	99	17.4	11.0
Octopus										1	0.4	2.3	1	0.2	0.7
Other Prey*				**29**		**31.3**	**1**		**1.9**				**30**		**4.4**
Bird													0		0.0
Polychaete worm				29		31.3	1		1.9				30		4.4

* Polychaete worms and birds were considered to be secondary or incidental prey items and therefore not included in the calculations of percent numerical abundance.

significantly more Atka mackerel ($\chi^2 = 39.13, p < 0.001$) and pollock ($\chi^2 = 10.18, p = 0.001$) than breeding NFS.

Diet composition varied between scats and spews (Table 4). The occurrence of pollock ($\chi^2 = 11.18, p < 0.001$) and cephalopods ($\chi^2 = 5.58, p = 0.018$) was significantly higher in spews than in scats. Atka mackerel ($\chi^2 = 4.38, p = 0.036$) and northern smoothtongue ($\chi^2 = 4.43, p = 0.039$, Fisher's exact test) occurred more frequently in scats than in spews. The application of numerical correction factors to the scat MNI values resulted in a change in dominance ranks (Table 5).

Scats from breeding and non-breeding NFS contained a mean of 2.1 ± 0.1 and 1.7 ± 0.1 prey species and 5.2 ± 0.8 and 2.7 ± 0.3 individual prey items, respectively. Neither difference was significant ($p > 0.05$, Fligner–Policello tests). Nearly identical percentages (49.1%) of the scats from breeding NFS and non-breeding (48.8%) NFS contained only 1 prey species. The majority of scats from breeding NFS (80.9%) contained ≤ 5 individual prey items and 7.2% contained between 20 and 53 individual prey items. The majority of scats from non-breeding NFS (87.2%) contained ≤ 3 individual items with a maximum number of individual items in a single scat equaling 15. The number of prey species contained in spews from breeding (3.4 ± 0.2) and non-breeding (2.3 ± 0.1) NFS was not significantly different, nor were there significant differences in the number of prey species found in scats from breeding (2.6 ± 0.1) and non-breeding NFS (3.1 ± 0.1, $p >$ 0.05, Fligner–Policello tests).

The *MNI* of prey items differed between scats and spews (Table 6). The *MNI* of Atka mackerel ($\hat{U} = -3.15, p = 0.002$), cephalopods ($\hat{U} = -3.99, p < 0.001$), and pollock

Table 4. Results of logistic regression models comparing occurrence of prey species found in Steller sea lion (SSL) scats and northern fur seal (NFS) scats and spews. Odds ratios (OR) indicate relative magnitude of relationship. B = breeding, NB = non-breeding. Degrees of freedom = 1 for all tests.

	NFS-B vs NFS-NB			NFS-B vs SSL			NFS-NB vs SSL			NFS Scats vs Spews		
Prey	χ^2	**p**	**OR**	χ^2	**p**	**OR**	χ^2	**p**	**OR**	χ^2	**p**	**OR**
Atka Mackerel	39.13	< 0.001	0.14	94.91	< 0.001	0.06	7.53	0.006	0.39	4.38	0.036	2.22
Cephalopods	29.76	< 0.001	6.64	55.94	< 0.001	8.50	0.54	0.463	1.32	5.58	0.018	0.39
N. Smoothtongue	20.41	< 0.001	6.47	22.02	< 0.001	120.00	7.49	0.006	18.55	4.43[a]	0.039	
Pollock	10.18	0.001	0.38	1.17	0.280	0.733	6.26	0.012	1.95	11.18	< 0.001	0.306
Salmon	6.70	0.010	1.98	34.07	< 0.001	3.99	7.89	0.005	2.01	—[b]		

[a]Not analyzed in logistic regression model due to quasi-separation of the data. Pearson's chi-square with Fisher's exact test reported here.
[b]Not included in the final model due to lack of significance.

Table 5. Summary of adjusted numerical abundance (NA*) based on prey- and size-specific numerical correction factors applied to the minimum number of individuals consumed for the five most commonly occurring prey types. Each prey type is ranked based on frequency of occurrence (FO), numerical abundance based on scats only (NA^s), and adjusted numerical abundance.

	Northern fur seals Breeding			Northern fur seals Non-breeding			Steller sea lions		
Prey type	NA^s	**NA* (95% CI)**	**Rank FO / NA^s / NA***	NA^s	**NA* (95% CI)**	**Rank FO / NA^s / NA***	NA^s	**NA* (95% CI)**	**Rank FO / NA^s / NA***
Atka mackerel	9.9	11.7 (9.1, 15.5)	3 / 4 / 3	48.7	53.0 (41.1, 70.2)	1 / 1 / 1	76.8	79.5 (62.0, 100.0)	1 / 1 / 1
Cephalopods	27.4	18.1 (17.7, 18.6)	2 / 2 / 2	9.1	5.4 (5.4, 5.7)	4 / 4 / 5	3.9	2.3 (2.2, 2.3)	4 / 4 / 4
Northern Smoothtongue	48.4	55.1 (46.7, 67.7)	4 / 1 / 1	6.0	6.4 (5.4, 7.7)	5 / 5 / 4	0.3	0.3 (0.2, 0.3)	5 / 5 / 5
Pollock	3.6	3.9 (2.2, 6.4)	5 / 5 / 5	23.3	22.9 (13.6, 38.3)	2 / 2 / 2	10.9	10.4 (6.2, 18.0)	2 / 2 / 2
Salmon	10.8	11.2 (8.2, 17.7)	1 / 3 / 4	12.9	12.3 (9, 19.5)	3 / 3 / 3	8.2	8.2 (5.4, 11.7)	3 / 3 / 3

Table 6. Summary of the comparison of minimum number of individual prey items consumed between northern fur seals (NFS) and Steller sea lions (SSL). Values are mean ± SEM (min, max).

Prey	NFS			SSL	Fligner-Policello test		
	Spew	Scat	Total	Total	NFS scat *vs* spew	NFS scat *vs* SSL scat	NFS total *vs* SSL scat
Atka mackerel	2.9 ± 0.5 (1, 9)	1.5 ± 0.1 (1, 6)	1.8 ± 0.1 (1, 9)	2.5 ± 0.1 (1, 10)	$\hat{U} = -3.15$ $p = 0.002$	$\hat{U} = -6.21$ $p < 0.001$	$\hat{U} = -5.68$ $p < 0.001$
Cephalopod	8.2 ± 2.5 (1, 35)	2.9 ± 0.4 (1, 23)	4.2 ± 0.7 (1, 35)	1.3 ± 0.2 (1, 5)	$\hat{U} = -3.99$ $p < 0.001$	$\hat{U} = 5.66$ $p < 0.001$	$\hat{U} = 8.01$ $p < 0.001$
N. Smoothtongue	1.3 ± 0.3 (1, 2)	7.4 ± 1.6 (1, 53)	6.8 ± 1.5 (1, 53)	2.0 ± 0.0 (2, 2)	$\hat{U} = 2.60$ $p = 0.009$	N/A	N/A
Pollock	3.3 ± 0.6 (1, 11)	1.6 ± 0.3 (1, 12)	2.2 ± 0.3 (1, 12)	1.6 ± 0.2 (1, 5)	$\hat{U} = -4.56$ $p < 0.001$	$\hat{U} = -0.98$ $p = 0.328$	$\hat{U} = 1.30$ $p = 0.195$
Salmon	1.0 ± 0.0 (1, 1)	1.1 ± 0.1 (1, 3)	1.1 ± 0.1 (1, 3)	1.2 ± 0.1 (1, 3)	$\hat{U} = 1.88$ $p = 0.060$	$\hat{U} = -2.29$ $p = 0.022$	$\hat{U} = -2.45$ $p = 0.014$

($\hat{U} = -4.56, p < 0.001$) consumed were significantly higher in spews than in scats. Scats contained a significantly higher number of northern smoothtongue than spews ($\hat{U} = 2.60$, $p = 0.009$). There was no difference in salmon *MNI* between scats and spews ($\hat{U} = 1.88, p = 0.060$). Atka mackerel was the prey type found in 71.4% of scats from non-breeding NFS that contained only one species, while scats from breeding NFS that contained only one prey type were more likely to contain salmon (40.7%) than any other taxon.

In samples from breeding NFS, the occurrence of Atka mackerel was significantly negatively correlated with the occurrence of cephalopods ($r = -0.23$, $t_{0.05(3),124} = -2.58, p = 0.010$; Figure 4) and salmon ($r = -0.26$, $t_{0.05(3),124} = -2.94, p = 0.003$), and positively correlated with pollock ($r = 0.24$, $t_{0.05(3),124} = 2.67, p = 0.008$). In samples from non-breeding NFS, Atka mackerel was negatively correlated with pollock ($r = -0.43$, $t_{0.05(3),118} = -5.02, p < 0.001$). Northern smoothtongue was positively correlated with cephalopods in samples from both breeding ($r = 0.30$, $t_{0.05(3),124} = 3.38, p = 0.001$) and non-breeding NFS ($r = 0.24$, $t_{0.05(3),122} = 2.68, p = 0.007$).

Sea lion diet

Of the 271 scats collected from SSL, 247 (91.1%) contained prey remains that could be minimally identified to the family level. A total of 14 different prey were identified with six to species. The most common prey items (Table 7), in order of both frequency and abundance, were Atka mackerel (*FO* = 87.1%, *NA* = 71.8%), walleye pollock (*FO* = 19.6%, *NA* = 10.2%) salmon (*FO* = 19.2%, *NA* = 7.8%), and cephalopods

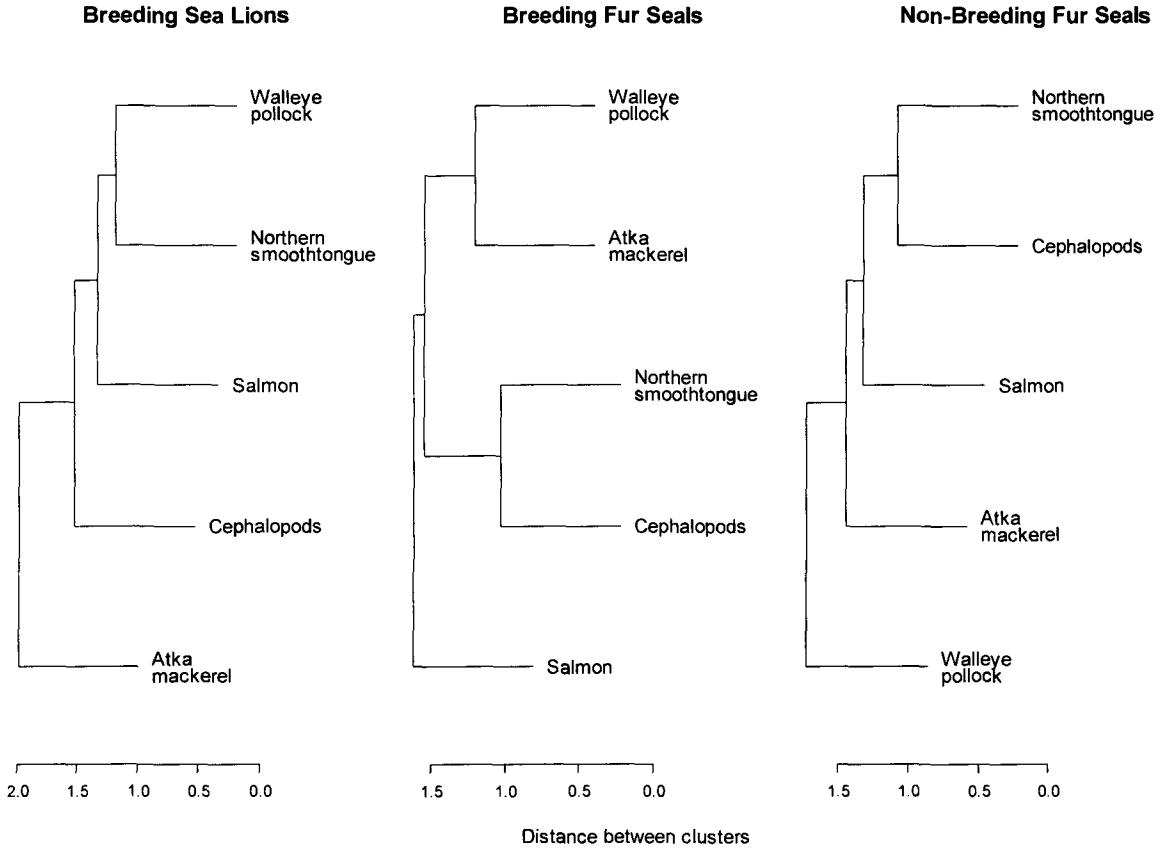

Figure 4. Clustering dendrograms of prey groups found in Steller sea lion and northern fur seal scats collected on Lovushki Island, Russia, during the breeding seasons of 2003, 2005, 2007, and 2008.

Table 7. Minimum number of individual prey items consumed (MNI), percent numerical abundance (NA), and percent frequency of occurrence (FO) of prey taxa found in scats and spews from breeding Steller sea lions collected on Lovushki Island during the breeding seasons of 2003, 2005, 2007, and 2008. The total number of samples collected and the total number of samples with prey remains are in parentheses. Grouped totals are in bold.

	2003 (n =32/32)			2005 (n = 53/53)			2007 (n = 111/111)			2008 (n = 75/75)			Total (n =271/271)		
Prey Type	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**	**MNI**	**NA**	**FO**
Fish	**73**	**98.6**	**100.0**	**170**	**97.1**	**100.0**	**308**	**98.1**	**100.0**	**216**	**91.9**	**100.0**	**767**	**96.4**	**99.6**
Unidentified fish	4	5.4	12.5	2	1.1	3.8	8	2.5	7.2	8	3.4	10.8	22	2.8	8.1
Hexagrammidae	**57**	**77.0**	**84.4**	**118**	**67.8**	**77.4**	**245**	**78.0**	**91.0**	**154**	**65.5**	**90.5**	**574**	**72.1**	**87.1**
Atka mackerel	56	75.7	84.4	118	67.8	77.4	244	77.7	91.0	154	65.5	90.5	572	71.9	87.1
Greenling sp.	1	1.4	3.1				1	0.3	0.9				2	0.3	0.7
Gadidae	**5**	**6.8**	**12.5**	**18**	**10.3**	**26.4**	**24**	**7.6**	**13.5**	**42**	**17.9**	**32.4**	**89**	**11.3**	**21.0**
Unidentified gadid										1	0.4	1.4	1	0.1	0.4
Walleye pollock	3	4.1	9.4	16	9.2	24.5	24	7.6	13.5	38	16.2	29.7	81	10.2	19.6
Pacific cod	2	2.7	3.1	2	1.1	3.8				4	1.7	5.4	8	1.0	2.6
Salmon	5	6.8	15.6	29	16.7	41.5	24	7.6	18.9	4	1.7	5.4	62	7.8	19.2
N. smoothtongue										2	0.9	1.4	2	0.3	0.4
Other fish species	**2**	**2.7**	**3.1**	**3**	**1.7**	**5.7**	**7**	**2.2**	**5.4**	**7**	**3.0**	**9.5**	**19**	**2.4**	**6.3**
Antlered sculpin							1	0.3	0.9				1	0.1	0.4
Sculpin sp.										1	0.4	1.4	1	0.1	0.4
Herring	1	1.4	3.1										1	0.1	
Irish lord sp.				1	0.6	1.9	1	0.3	0.9	1	0.4	1.4	3	0.4	1.1
Flatfish sp.	1	1.4	3.1							2	0.9	2.7	3	0.4	1.1
N. Lampfish				1	0.6	1.9				2	0.9	2.7	3	0.4	1.1
Lampfish sp.							1	0.3	0.9				1	0.1	0.4
Prickleback sp.				1	0.6	1.9	1	0.3	0.9	1	0.4	1.4	3	0.4	1.1
Sand lance							1	0.3	0.9				1	0.1	0.4
Snailfish sp.							2	0.6	1.8				2	0.3	0.7
Cephalopods	**1**	**1.4**	**3.1**	**5**	**2.9**	**9.4**	**6**	**1.9**	**5.4**	**17**	**7.2**	**14.9**	**29**	**3.6**	**8.5**
Unidentified ceph.				4	2.3	7.5	2	0.6	1.8	4	1.7	5.4	10	1.3	3.7
Squid sp.	1	1.4	3.1	1	0.6	1.9	4	1.3	3.6	12	5.1	9.5	18	2.3	4.8
Octopus sp.										1	0.4	1.4	1	0.1	0.4
Other Prey*	**1**		**3.1**	**3**		**3.8**	**5**		**2.7**				**9**		**2.2**
Bird sp.							1		0.9				1		0.4
Polychaete worm	1		3.1	3		3.8	4		1.8				8		1.8

* Polychaete worms and birds were considered to be secondary or incidental prey items and therefore not included in the calculations of percent numerical abundance.

(*FO* = 8.5%, *NA* = 3.8%). The primary squid species consumed was *Gonatopsis* sp. cf. *G. borealis*.

Scats from SSL contained a mean of 1.6 ± 0.06 prey species and 3.1 ± 0.14 individual prey items. Over half (57.7%) of the scats contained only 1 prey species and of these, 94.1% contained Atka mackerel. The majority of scats (89.4%) contained ≤ 5 individual prey items. The occurrence of Atka mackerel was significantly negatively correlated with the occurrence of pollock ($r = -0.29$, $t_{0.05(3),256} = -4.86$, $p < 0.001$; Figure 4), salmon ($r = -0.30$, $t_{0.05(3),\ 256} = -5.06$, $p < 0.001$) and northern smoothtongue ($r = -0.56$, $t_{0.05(3),\ 256} = -10.66$, $p < 0.001$). Northern smoothtongue was significantly correlated with pollock ($r = 0.21$, $t_{0.05(3),\ 256} = 3.40$, $p = 0.001$) and salmon ($r = 0.18$, $t_{0.05(3),\ 256} = 2.87$, $p = 0.004$).

Niche overlap and diet diversity

SSL consumed significantly more Atka mackerel than both breeding ($\chi^2 = 94.91$, $p < 0.001$) and non-breeding ($\chi^2 = 7.53$, $p = 0.006$) NFS. Breeding NFS consumed significantly more cephalopods ($\chi^2 = 55.94$, $p < 0.001$), northern smoothtongue ($\chi^2 = 22.02$, $p < 0.001$), and salmon ($\chi^2 = 34.07$, $p < 0.001$) than SSL. Non-breeding NFS consumed significantly more smoothtongue ($\chi^2 = 7.49$, $p = 0.006$) and salmon ($\chi^2 = 7.89$, $p = 0.005$) than SSL (Table 4).

Pianka's niche overlap index for breeding and non-breeding fur seals based on scats and spews combined was 0.468. Based on NA^s and NA^*, breeding and non-breeding

NFS had a niche overlap index of 0.385 and 0.359, respectively. The niche overlap index was 0.230 for SSL and breeding NFS based on scats alone and 0.947 for SSL and non-breeding NFS. These two overlap index values were significantly different ($p < 0.05$). All overlap indices differed only slightly when based on *NA* instead of NA^* (Table 8).

The sizes of prey items occurring in ≥5% of scats did not differ between SSL and non-breeding NFS when only scats were considered (Atka mackerel: $\chi^2 = 4.47$, $p = 0.502$; pollock: $\chi^2 = 1.12$, $p = 0.812$; salmon: $\chi^2 = 3.60$, $p = 0.152$). The sizes of Atka mackerel consumed by SSL and non-breeding NFS were significantly different when both scats and spews were considered ($\chi^2 = 11.77$, $p = 0.035$), with SSL consuming a higher proportion of small (16–20 cm) Atka mackerel ($\chi^2 = 6.46$, $p = 0.011$) and NFS consuming a higher proportion of medium-large (29–35 cm) Atka mackerel ($\chi^2 = 5.86$, $p = 0.015$). There were no differences in sizes of salmon ($\chi^2 = 3.23$, $p = 0.219$) or pollock ($\chi^2 = 2.54$, $p = 0.519$) consumed when both scats and spews were considered (Figure 5).

Shannon's diet diversity index for breeding and non-breeding NFS, based on scats and spews, was 1.321 and 1.378 respectively. Overall, NFS had a diet diversity index of 3.085 based on scats and spews. Based on scats alone, breeding and non-breeding NFS had a diet diversity index of 1.296 and 1.341, respectively. The overall diet diversity index for NFS based on scats alone was 3.389. SSL had a diet diversity index of 0.794, which was significantly different from both the breeding and non-breeding NFS diet diversity indices (Table 9).

Table 8. Summary of Pianka's niche overlap indices calculated using three different measures of numerical abundance for breeding (B) and non-breeding (NB) northern fur seals (NFS) and Steller sea lions (SSL).

	Niche overlap index (O_{jk}) (95% CI)		
Groups (*i*, *h*)	**NA**	**NA_s**	**NA***
SSL, NFS	0.539	0.539	0.520
	(0.324, 0.650)	(0.324, 0.650)	(0.324, 0.696)
SSL, NFS-B	0.218	0.227	0.230
	(0.124, 0.305)	(0.107, 0.330)	(0.086, 0.352)
SSL, NFS-NB	0.831	0.937	0.947
	(0.710, 0.974)	(0.877, 1.000)	(0.896, 1.000)
NFS-B, NFS-NB	0.468	0.385	0.359
	(0.287, 0.673)	(0.228, 0.529)	(0.293, 0.679)

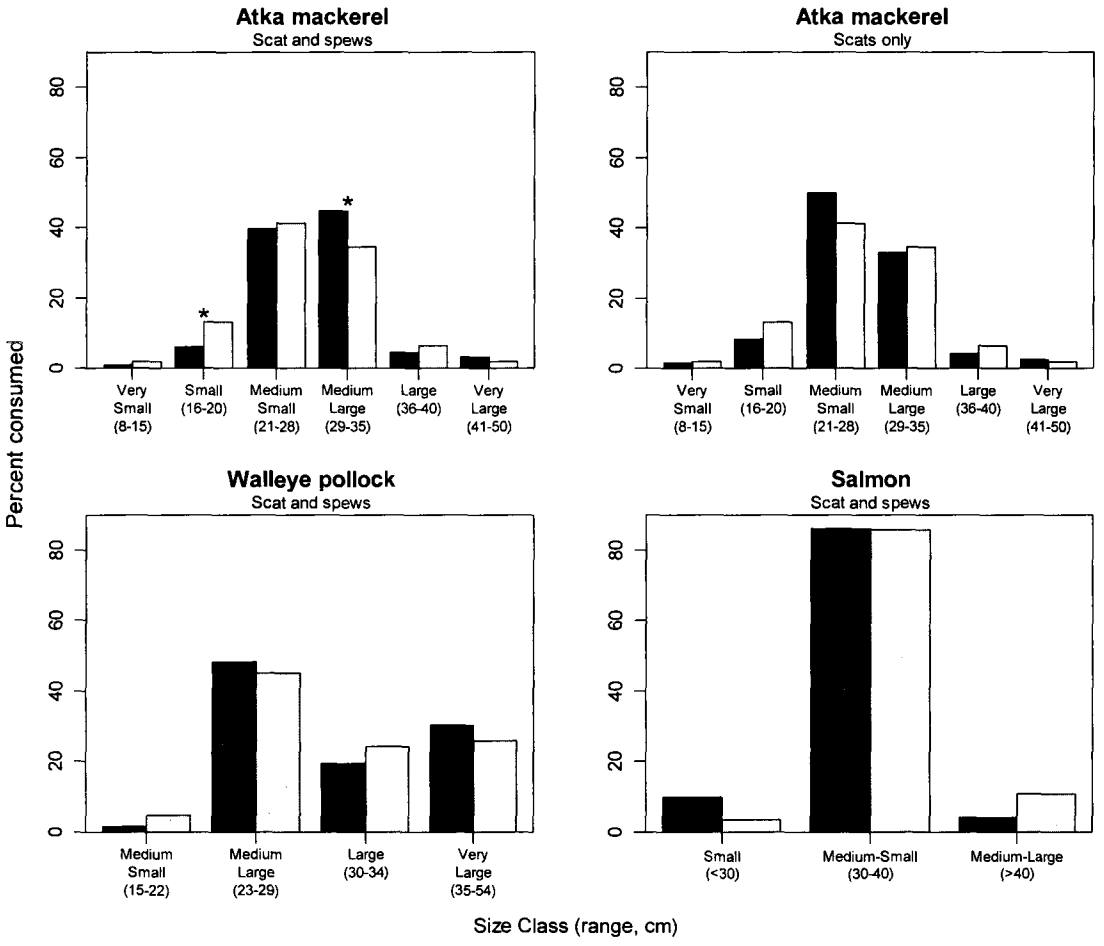

Figure 5. Sizes of prey items consumed by non-breeding northern fur seals (black) and breeding Steller sea lions (grey) during the breeding seasons of 2003, 2005, 2007, and 2008. Asterisks (*) indicates a significant difference.

Table 9. Summary of Shannon's index of diversity calculated for breeding (B) and non-breeding (NB) Steller sea lions (SSL) and northern fur seals (NFS) using numerical abundance of prey remains calculated from all samples (NA) and from scat samples only (NA_s).

	Diet diversity (H) (95% CI)	
Group	**NA**	**NA_s**
SSL	0.794	0.794
	(0.698, 0898)	(0.698, 0898)
NFS	3.085	3.389
	(2.310, 5.000)	(2.333, 5.000)
NFS-B	1.321	1.296
	(1.255, 1.434)	(1.213, 1.432)
NFS-NB	1.378	1.341
	(1.277, 1.542)	(1.200, 1.527)

DISCUSSION

Inter-specific competition

This study found significant differences between the diets of breeding NFS and SSL such that breeding SSL consumed primarily Atka mackerel, while breeding NFS consumed primarily northern smoothtongue and cephalopods. This difference in prey selection between NFS and SSL is likely reflective of the different diving abilities and provisioning strategies of the two species, as well as the fasting abilities of their dependent young (Costa *et al.* 2005).

Larger diving animals have greater oxygen stores and lower mass-specific rates of oxygen consumption, and therefore make longer and deeper dives than smaller divers. A model by Mori (2002) predicts that, to forage optimally, smaller divers should seek prey at shallower depths. Additionally, small pinnipeds are adapted to exploiting locally abundant and predictable sources of prey while larger pinnipeds are more adapted to exploiting more dispersed prey (Costa 1993). Thus, NFS that prey on abundant prey species such as cephalopods and northern smoothtongue that aggregate in large numbers near the surface at night may be optimizing their foraging strategy, leaving non-schooling prey items that occur at deeper depths, such as Atka mackerel, to the larger SSL.

To maximize their fitness, central place foragers must maximize their energy intake while minimizing their energy expenditure in order to deliver the maximum amount of nutrients and energy to their dependent pups (Pyke *et al.* 1977). However,

fitness is not always maximized by feeding on the most energy-dense prey species. In addition to choosing which species to consume, an optimally foraging predator may also modify its behavior in order to choose the optimal foraging location (Pyke *et al.* 1977). Optimal foraging location may be selected as a consequence of either reduced foraging costs or a reduction in the local availability of prey, such as might occur when competition levels are high. To maintain a consistent supply of energy to their young, a central place forager must deliver more energy per foraging trip as the distance to the foraging grounds and trip duration increases (Arnould and Boyd 1995). A patch of prey with a lower net rate of energy gain may be selected by central place foragers if it is close to the rookery, thereby reducing overall energy expenditure through a reduced cost of transport (Staniland 2007). Atka mackerel are a medium-energy prey species; specimens collected in the western Aleutian Islands, with an average mass of 694.8 g, contained an average of 5.6 $kJ \cdot g^{-1}$ (wet weight) of energy and 6.9% lipid (Logerwell and Schaufler 2005). Atka mackerel are pelagic throughout most of the year but become demersal and migrate to shallow waters in the summer to spawn, living at depths from the inter-tidal zone to <200 m (Gorbunova 1962, McDermott and Lowe 1997). Atka mackerel are a relatively cryptic species, often hiding amongst the rocks and kelp during the spawning season (Gorbunova 1962), which may increase the amount of time required to be located and captured by predators (Bowen *et al.* 2002). Thus, while SSL foraging on Atka mackerel may have a relatively lower rate of energy gain on a per-dive basis, they have an overall lower cost of foraging associated with reduced travel between the rookery and the foraging grounds and can therefore deliver energy in the form of milk to their pups on

a more frequent basis. However, in order to support this foraging strategy, sea lions require a locally abundant prey source (Boyd 1998). A local abundance of Atka mackerel is supported by the low diet diversity index for SSL calculated in this study, which suggests a high abundance of the preferred food item and, therefore, greater specialization (Pyke *et al.* 1977, Waite and Burkanov 2006).

In contrast, squid and northern smoothtongue consumed by NFS in this study are mid-water shelf and mesopelagic prey items located relatively far offshore, requiring longer foraging trip durations and, therefore, higher levels of energy expenditure associated with travel costs. As foraging trip duration increases, it is necessary for NFS to acquire more energy per trip in order to maintain a constant supply of energy to their pups. Additionally, pinnipeds on longer foraging trips spend proportionately less time diving and thus need to increase the net energy gained per dive (Staniland 2007). Northern smoothtongue are a deep-water smelt with a high energy density; samples collected in the central Bering Sea in June of 2000 had an average energy density of 8.37 $kJ \cdot g^{-1}$ wet weight (Davis 2003). Smoothtongue are located at depths of 200–1000 meters during the day but migrate to the 0–200 m at night (Sobolevskii and Sokolovskaya 1994, Sobolevsky *et al.* 1996). Commander squid collected in the western Aleutian Islands were of a lower energy value, containing an average of 3.95 $kJ \cdot g^{-1}$ (wet weight) of energy and 3.65% lipid (Logerwell and Schaufler 2005). Partial squid samples collected from stomach contents of NFS on Lovushki Island ($n = 3$) contained an average of 2.58 ± 0.44% lipid (J. Waite, unpublished data). Like smoothtongue, many squid species migrate vertically and aggregate in large numbers at the surface at night, especially during

spawning (Moiseev 1991, Lapko 1996, Watanabe *et al.* 2006) and, although they are not as energy-dense, large numbers can be easily captured in a short amount of time. Between the high-energy smoothtongue and the abundant squid, it is likely that NFS have a relatively high rate of energy gain per dive.

In response to reduced prey availability, such as might occur when competition for prey resources is high, predators can choose to either modify their prey choice or foraging location, or increase their foraging effort. Costa and Gentry (1986) found that during periods of reduced prey availability, northern fur seals on St. George Island, Alaska, increased their foraging effort rather than trip duration, the latter of which should be done only as a last resort (Costa 2008). However, optimal patch choice is partly decided by the extent of competition for prey within a given area (Pyke *et al.* 1977) and the ability of fur seals to modify foraging behavior varies between rookeries (Costa 2008). Therefore, the breeding NFS in the present study may have chosen to increase their trip duration to exploit richer prey sources in response to competition with the larger SSL or the abundant juvenile NFS.

There was a biologically significant overlap in the diets of SSL and non-breeding NFS, indicating the potential for strong inter-specific competition for food resources. When only scats were considered, there were no significant differences in the sizes of prey consumed by SSL and non-breeding NFS. When both scats and spews were considered, significantly more Atka mackerel in the 29–35 cm size class were found in NFS samples. This may be an artifact of larger prey items being regurgitated rather than passing through the gastrointestinal tract. However, an organism's niche is a multi-

dimensional concept, which includes variables such as prey selection, foraging location, and time budgets. Niche overlap indices, such as Pianka's niche overlap index, take into account only a single dimension at a time and may not closely relate to the true overall niche overlap. Therefore, a strong overlap in prey selection may not necessarily indicate strong competition if there is little overlap between other niche dimensions, such as foraging location. Further studies on these other dimensions, such as the deployment of satellite-linked time-depth recorders on both groups, or detailed examination of the energetic requirements of both groups, need to be completed before the potential level of competition between these two groups can be fully assessed.

Intra-specific competition

There was a clear difference between the diets of breeding and non-breeding fur seals. This is likely a reflection of the difference in energetic and time constraints between the two groups rather than a direct means by which to reduce intra-specific competition. Lactating females need to carefully balance their time and energy budgets in order to meet their basic nutritional demands, as well provide sufficient energy to their dependent pups. Non-breeding animals have fewer restrictions with regards to the resources they can exploit and the amount of time spent doing so.

Study biases

Studies conducted on a variety of captive pinnipeds have confirmed the use of scat and spew analyses as a practical and accurate means by which to assess prey selection and numerical proportion of different prey species (Dellinger and Trillmich 1988, Fea and Harcourt 1997, Orr and Harvey 2001, Tollit *et al.* 2003). However, the use of undigested prey remains recovered from scats and spews has inherent biases which need to be taken into consideration during data analysis and interpretation. Of primary concern are the digestibility differences among prey species. Although Arim and Naya (2003) derived an opposite conclusion using a mathematical model, most empirical studies show that smaller prey species are more likely subject to complete digestion, which may lead to prey under-representation (Dellinger and Trillmich 1988, Gales and Cheal 1992). Skeletal elements from larger prey remains may accumulate in the stomach over time before being regurgitated. Therefore, spew samples may provide an overestimation of larger prey items or prey with especially robust skeletal elements. Combining data from scats and spews have been reported to reduce these errors (Gudmundson *et al.* 2006). The application of numerical correction factors (NCFs) may also help minimize the bias associated with differential digestion (Bowen 2000, Orr and Harvey 2001, Lundström *et al.* 2007). We applied NCFs developed by Tollit *et al.* (2007) through experiments with captive SSL to SSL scat samples collected for this study. These particular correction factors were chosen because they were based on the recovery of all identifiable skeletal elements, rather than relying solely on recovered otoliths and are

therefore applicable to samples where only non-otolith elements were recovered. There are currently no published NCFs based on all skeletal elements developed specifically for NFS for the range of prey species identified in the samples collected on Lovushki Island. Correction factors are available for other fur seal species; however, they are either based only on recovered otoliths or were developed for fur seal species that forage on a substantially different prey (Bowen 2000, Staniland 2002). Therefore, due to their similar diets and digestive physiologies (Ridgway 1972), as well as the fact that the majority of prey items were identified using skeletal elements other than otoliths, the NCFs developed for SSL were also applied to the NFS scat samples.

Digestion rates are also affected by meal size, feeding frequency, diet mixing, and prey quality (Hunt and Stubbs 1975, Markussen 1993, Trumble *et al.* 2003, Trumble and Castellini 2005). Smaller meals, meals consisting primarily of lower energy density prey, or infrequent meals, may move through the gastrointestinal tract at a slower rate to maximize the absorption of nutrients into the body. Thus, skeletal elements of prey items in the throughput of smaller meals are subjected to higher levels of erosion. In contrast, larger meals, meals consisting of higher energy density prey, or frequent meals, have decreased transit times increasing the likelihood of passing hard parts intact. This may be an especially important consideration when comparing the diets of lactating and non-lactating central place foragers. Breeding females must maximize their energy intake in order to provide enough energy to their young as well as to meet their own energetic requirements. It would be logical to assume that between fasting periods on the rookery, females may attempt to maximize their meal size and the quality of prey items during

intermittent foraging. Juvenile and other non-breeding animals are not under such energetic and time constraints and could therefore consume several smaller, more frequent meals over a period of time to meet their energetic requirements.

Other potential biases include partial consumption of prey items, deposition of remains from a single meal over multiple samples, and voiding of scats and spews while at sea. Larger prey items, especially salmon (Hauser *et al.* 2008), are often brought to the surface and torn apart prior to consumption. In many of these cases, the head is discarded, emphasizing the importance of using elements other than otoliths for prey identification (Hauser *et al.* 2008). Unfortunately, many of the skeletal elements, such as vertebrae, teeth, and gillrakers, are not useful for the enumeration of prey items consumed. Thus, the number of prey items eaten in this fashion may be underestimated. Numerical correction factors may partially correct for this type of bias. Elements from prey items consumed in a single meal can be deposited in multiple scats over a period of days. The collection of only fresh, intact samples reduced the chance of counting the same prey item more than once and overestimating the frequency of occurrence of that particular prey species. Tollit *et al.* (2003) found the initial defecation time for a meal fed to captive SSL to be between 2–56 hours and skeletal elements from prey items were found in scats up to 148.3 hours after feeding. The mean final defecation time for a single meal was 82 ± 41 hours. As foraging trips can exceed this time frame (Robson *et al.* 2004, Call *et al.* 2008), meals consumed during the early stages of foraging may be voided at sea. Scats and spews deposited on land, therefore, may be reflective of meals consumed only during the later stages of the foraging trip or of prey items consumed on the return trip.

Depending on the distance traveled, meals consumed at the primary foraging location may be entirely voided prior to returning to the rookery.

The limited number of samples collected during the study period also presents a potential bias. Collecting large numbers of scat and spew samples from a northern fur seal rookery is not a trivial task. Unlike Steller sea lions, breeding northern fur seals are not easily displaced. Bulls will quickly and aggressively attack intruders and are difficult to move from their territories and female fur seals will vigorously defend their pups. Therefore, to reduce the chance of injury to both animals and researchers, collection of samples from breeding fur seals was limited to the few times when the rookery was cleared during mass exodus to the water. Even during these times, the area cleared was usually quite small as bulls would attempt to reclaim their territories within minutes. Thus, the time available for scat and spew collection was also extremely limited. The use of a mobile, protective cage, commonly used to move around some fur seal rookeries (Boltnev and Stus 1998), was not practical on Lovushki Island due to the rocky, uneven terrain. The terrain itself also limited the number of samples collected for both SSL and NFS. Tidal action routinely flooded substantial portions of the rookery and wave action quickly washed away samples near the waterline. Samples that were deposited above the flood zone and out of reach of the waves were quickly trampled or lost between cobbles. Although the number of intact, fresh samples was very limited, the total number collected over the course of the study was considered sufficient to ensure that a difference between two populations was found to be statistically significant with at least 80% power at the 5% level for prey items occurring in >5% of scats (Trites and Joy 2005).

CONCLUSIONS

The SSL on Lovushki Island have a very specialized diet. This is illustrated in both the high frequency of occurrence and numerical dominance of their primary prey item, Atka mackerel, as well as in their foraging tactics inferred from both the location of their primary prey and the negative correlation between the occurrence of Atka mackerel in SSL scat and all other prey types. The diet of breeding NFS, while more diverse than SSL, suggests a specialization on squid and northern smoothtongue. This clear partitioning of prey items and foraging location between breeding animals allows both to coexist within the same geographical region despite an increase in the population of both predator species.

The diet of non-breeding NFS is more representative of a generalist predator but there is a significant overlap with SSL in prey species and prey sizes consumed. As non-breeding NFS outnumber the SSL by an order of magnitude, there is substantial potential for inter-specific competition for dietary resources between these two groups. While non-breeding NFS may have greater flexibility to modify their foraging strategy due to differences in energetic demands, a continued rapid increase in the NFS population could bring about localized shortages in the primary prey items of SSL, forcing the SSL to either increase their nearshore foraging efforts or to begin foraging further offshore on more pelagic prey species. Either option would cause the SSL to expend larger amounts of energy over the course of a foraging trip and would increase the amount of time the SSL pups must fast between meals. Additionally, an expanded foraging range and

increase in the consumption of other prey items by SSL may increase the dietary niche overlap and inter-specific competition with breeding NFS and may have negative consequences for the population of either species. Continued growth of the NFS population on Lovushki Island may lead to the competitive exclusion of SSL due to inter-specific competition for food resources.

CHAPTER 2. BIOCHEMICAL ANALYSES OF VIBRISSAE AND BLUBBER

INTRODUCTION

Steller sea lions (SSL, *Eumetopias jubatus*) breed sympatrically with northern fur seals (NFS, *Callorhinus ursinus*) on the Lovushki (48.5436° N, 153.6736° E) Island group in the Kuril Island chain. As in North American waters, the Asian subpopulation of SSL experienced a dramatic decline and has been unstable for the past four decades (Loughlin *et al.* 1992, Burkanov and Loughlin 2005). After experiencing an 81% decline in population from 1955–1989 followed by a slight increase, the abundance of non-pup SSL on Lovushki Island has remained relatively stable at an average of 1039 SSL from 1995 through 2005 (Burkanov and Loughlin 2005). The NFS population also experienced a period of relative stability from approximately 1978–1988 (Kuzin 1999); however, a rapid increase in NFS population numbers ensued during the early 21st century, and the pup population grew to 12,180 pups by 2006 (Burkanov *et al.* 2007), placing the non-pup population on Lovushki Island at an estimated 28,420 adult and juvenile NFS.

The competitive exclusion principle postulated by Gause (1934) maintains that one of two non-interbreeding species occupying the same ecological niche will be displaced if population growth is not the same between species. Thus, competition may result in the absolute exclusion of one of the species unless this species is able to modify how it exploits the available resources. SSL and NFS are both piscivorous, sexually dimorphic pinnipeds with similar ecological requirements and life history traits. With a

2–3 month overlap in breeding seasons (May–August) and pup nursing, foraging becomes competitive as adult females of both species are central place foragers, alternating between periods of foraging at sea and nursing their pups on land (Mathisen *et al.* 1962, Pitcher and Calkins 1981, Gentry and Kooyman 1986, Gentry 2002).

To accurately assess the level of dietary overlap, and thus competition for prey, between two sympatric species, it is often necessary to consider foraging behavior and prey consumption over a range of time scales. Distribution of prey items may change over the course of the breeding season, prompting a change in foraging effort by one or more of the resident predator species. Further, any one particular sampling effort may occur during an anomalous and/or ephemeral influx of a specific prey type, and depending on the type of sample collected, inferences regarding the overall dietary composition for the entire breeding season based on these data may be erroneous.

The composition of SSL and NFS diets has been determined primarily through the analysis of undigested prey remains recovered from stomach and intestinal contents, scats, and spews (Gudmundson *et al.* 2006, Waite and Burkanov 2006, Zeppelin and Ream 2006, Trites *et al.* 2007). However, there are a number of biases implicit to these techniques (see Dellinger and Trillmich 1988, Gales and Cheal 1992, Harvey and Antonelis 1994, Staniland 2002, Arim and Naya 2003). On Lovushki Island, where inter-specific spatial mixing of sympatric species occurs, it can be difficult to distinguish between scats of different predator species without molecular techniques (Waite *et al.* In press). Determination of diet among different age and reproductive groups can also be difficult when relying on scats. Furthermore, analysis of samples from a single collection

effort only provides information on prey consumed during the animal's most recent foraging trip and results may be biased by opportunistic feeding during the return trip from the primary foraging grounds or from voiding of gastrointestinal contents while at sea.

Naturally occurring stable nitrogen (^{15}N) and carbon (^{13}C) isotopes (SI) in pinniped tissues have been used successfully for the reconstruction of diets and trophic position (Hobson *et al.* 1997, Hall-Aspland *et al.* 2005, Dehn *et al.* 2007), estimation of foraging location (Burton and Koch 1999, Aurioles *et al.* 2006), and investigation of physiological condition and maternal strategies (Newsome *et al.* 2006, Sinisalo *et al.* 2008). The step-wise enrichment of ^{15}N in tissues of ~3–5‰ per trophic level allows for the estimation of an organism's relative trophic position in a food web (DeNiro and Epstein 1981, Minagawa and Wada 1984). Carbon isotope ratios are less significant in determining trophic position in marine mammals because of the weak isotopic fractionation of ^{13}C (~0.1–1.1‰) across trophic levels of higher level consumers (DeNiro and Epstein 1978, Hirons *et al.* 2001a, Kurle and Worthy 2001), but $\delta^{13}C$ levels can be used to determine relative foraging location. For example, $\delta^{13}C$ values tend to increase with latitude in the northern hemisphere and are higher in organisms occurring in benthic and nearshore habitats than those in pelagic and offshore habitats (France 1995, Hobson 1999, Kurle and Worthy 2002, Kurle and Gudmundson 2007).

Isotopic signatures of metabolically active tissues reflect recent feeding activity, whereas tissues with slower biochemical turnover rates integrate SI from the diet over longer periods of time (Hobson and Clark 1992, Kurle and Worthy 2002, Lesage *et al.*

2002). Serum has one of the fastest isotopic turnover rates (Lesage *et al.* 2002) and its SI signature corresponds to dietary assimilation from feeding activity within the previous 10–20 days (Hilderbrand *et al.* 1996, MacAvoy *et al.* 2006). However, the collection of serum (as well as most other tissues) is a fairly invasive procedure and the compilation of large sample sizes may be difficult. The isotopic composition of the biologically active portion of vibrissae (i.e., the root) reflects that of serum and also corresponds to recent feeding activity of SSL (Stegall *et al.* 2008). While SI analysis of vibrissae does not provide information on which specific prey species were consumed, examination of SI signatures along the length of the vibrissa can provide a time-integrated record of a predator's trophic level and general foraging location over the time period during which the vibrissae grew, possibly the entire lifespan of the animal (Hirons *et al.* 2001b).

The analysis of fatty acid (FA) profile in the blubber of pinnipeds can provide both qualitative and quantitative estimates of predator diets. Fatty acids are the primary constituents of lipids, and when consumed, the resultant FA profile of the predator adipose tissues closely reflects that of the prey consumed, and thus differences in FA composition of adipose tissue are largely a result of differences in prey consumption. FA analysis can be used qualitatively by examining differences in the FA composition between marine mammal predator species (Grahl-Nielsen *et al.* 2005, Thiemann *et al.* 2008), sexes (Beck *et al.* 2005, Meynier *et al.* 2008), among individuals (Iverson *et al.* 1997), between different spatial locations (Moller *et al.* 2000), or over time (Meynier *et al.* 2008). FA signatures may also be used to quantitatively estimate dietary intake by using statistical models to determine the combination of prey FAs that most closely

matches those of the predator (Iverson *et al.* 2004, Beck *et al.* 2007, Nordstrom *et al.* 2008).

The time period represented by the FA profile in the blubber of fur seals and sea lions may depend on the physiological condition of the animal at the time of sampling. During periods of heavy feeding and weight gain, usually outside of the breeding season, the FA profile may reflect either the current diet or an integration of dietary FA over periods of weeks to months (Iverson *et al.* 1997, Beck *et al.* 2005). During the breeding season, fur seals and sea lions undergo periods of fasting and depletion of blubber stores as lipids are mobilized for the production of milk for their pups. As fur seals and sea lions forage during their lactation period, FA composition of their blubber may be influenced by diet both before and during lactation (Wheatley *et al.* 2008).

Similar life history traits and ecological requirements, along with recent growth in the local population of both NFS and SSL, increase the potential for elevated inter-specific competition for food resources. This study examines the use of prey resources of sympatrically breeding SSL and NSF on Lovushki Island through the analysis of $\delta^{15}N$ and $\delta^{13}C$ stable isotope values of vibrissal roots and fatty acid profiles of blubber. We compare the results with data from concurrently collected scats and spews (Chapter 1) to assess the convergence of data representing different time scales and to gain further understanding of the foraging ecology and resource partitioning of these two species.

METHODS

Sample collection

During the breeding seasons of 2007 and 2008, vibrissae were collected from NFS ($n = 95$) and SSL ($n = 63$) on Lovushki Island, Russia (Figure 2). Of the NFS, samples were collected from 45 live adult females, 5 dead adult females, 23 live pups, and 20 dead pups. Vibrissae were also collected from a single dead adult NFS male and a dead NFS juvenile of unrecorded sex. Vibrissae collection from live adult animals was performed under gas anesthesia (Heath *et al.* 1996) whereas samples from pups were collected under manual restraint. Adult animals were anesthetized for 30–120 minutes while procedures were performed for concurrent research projects, such as attachment of telemetry instruments and deuterium oxide dilution for body composition analysis. Samples from dead animals were collected opportunistically on the rookery. Of the SSL samples, 19 were from live adult females, 9 dead adult females, 11 live pups, and 24 dead pups. From 2 adult female NFS and 4 adult female SSL, vibrissae were collected twice over a period of 4–6 weeks. Of the 158 animals sampled, vibrissae were collected from 21 NFS and 6 SSL mother-pup pairs. Sampling of vibrissae consisted of removing the longest vibrissa with root intact from the left cheek. Each vibrissa was measured (nearest mm) both before and after removal. On subsequent samplings of recaptured animals, the longest vibrissa on the right cheek was removed. All samples were air-dried and stored in paper envelopes at room temperature until analysis.

Concurrent with vibrissae collection, blubber biopsies were taken from live female NFS (n = 39) and SSL (n = 13) from the right ventral area just anterior to the rear flipper insertion point. SSL biopsies were collected during the second week of June in 2007 (n = 6) and third week of June in 2008 (n = 7). NFS samples were collected from the third week of June through the end of July in 2007 (n = 26) and during the third week of July in 2008 (n = 13). An additional five biopsies were collected remotely using a crossbow during the third week of July 2008 following Hoberecht *et al.* (2006), using a biopsy dart with a 35-mm-long biopsy tip for SSL and a 20-mm-long tip for NFS. Of these samples, 2 were from adult female SSL, 1 from a juvenile male SSL, and 2 from adult male NFS, resulting in a total of 41 NFS and 16 SSL blubber samples. Sampling location for remotely collected biopsies was the pectoral region, midway between the fore-flippers. Samples collected in 2007 were stored in 2.0 mL Cryovial tubes at -20°C. Samples collected in 2008 were flushed with nitrogen gas and stored in liquid nitrogen. All samples were transferred to -80°C upon returning from the field, approximately 1–2 months after collection.

Laboratory analyses

Vibrissae were soaked in a Branson 3510 ultrasonic water bath (Branson Ultrasonics Corporation, Danbury, Connecticut, USA) at 25°C for a minimum 10–20 minutes or until the root sheath was sufficiently softened to allow easy removal. The surfaces of the vibrissae were then cleaned with a solution of chloroform-methanol

volumetrically mixed at a 2:1 ratio to remove any contaminating lipids. The vibrissal roots were cut at 0.1–0.4 cm from the proximal end to obtain segments of 0.800–1.200 mg, which were weighed to the nearest 0.001 mg on a Sartorius CP2P scale (Sartorius AG, Goettingen, Germany) into Costech 3.5 × 5 mm pressed tin capsules (Costech Analytical, Valencia, California, USA). Stable isotopes were analyzed either on a Finnigan Delta V Plus mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA) coupled to a Carlo Erba elemental analyzer or a Finnigan Delta^{plus}XP mass spectrometer interfaced with a Costech ECS4010 elemental analyzer. Results are expressed in δ notation and are calculated as $\delta X = 1000 \times [(R_{sample} / R_{standard}) - 1]$, where δX is $\delta^{13}C$ or $\delta^{15}N$ in parts per thousand (‰) and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. Isotopic compositions are standardized relative to atmospheric N_2 for nitrogen and Vienna–Pee Dee Belemnite limestone for carbon.

FA methyl esters (FAME) were prepared as described in Iverson *et al.* (1997). Protocols for preparing and analyzing samples collected in 2008 for FAs using a Varian 3900 gas chromatograph-flame ionization detector (GC-FID) followed Budge *et al.* (2006) with the following modifications: Column CP-Select for FAME (CP7419) 100 m × 0.25 mm ID × 0.25 μm. The injector temperature was 250°C with a 1 μl injector split ratio of 50:1. Column flow was 1.0 ml min^{-1} programmed at 210°C for 9.0 min and ramped at 15°C min^{-1} to 260°C for 7.7 min. Detector temperature was set at 300°C with a hydrogen flow of 30 ml min^{-1} and air flow of 300 ml min^{-1}. The internal standard was C19:0 (Fluka 72332). Each fatty acid recovered was calculated as a percent of the

cumulative of all fatty acids in the blubber. A set of 40 standard historical marine FAME were used in the GC-FID analysis, and 38 were used with the GC-MS. The NIST (National Institute of Standards and Technology) library was utilized with GC-MS to confirm peaks matched with our standards, and additionally, to identify novel peaks using highest probability methods.

Blubber biopsies collected in 2007 were processed by a separate lab with the following modifications: FAs were extracted following Dodds *et al.* (2004) and analyzed on a HP 5890 Series II Plus (Hewlett-Packard, Palo Alto, CA) GC-FID using a 60 m × 0.25 mm ID × 0.25 μm DB-23 column. The injector temperature was 300°C with a 1 μl injector split ratio of 20:1. Column flow was 1.0 ml min^{-1} with temperature ramped from 125°C to 240°C at 3°C min^{-1} for a total runtime of 40.0 min. Peaks from 10% of the samples were verified with GC-MS on a Varian CP-3800 GC equipped with a Varian Saturn 2200 MS.

Statistical analyses

Analysis of variance (ANOVA) was used to examine equality of $\delta^{13}C$ and $\delta^{15}N$ isotope means between species (NFS or SSL), age class (adult female or pup, nested within species), and year (nested within age class). Repeated measures were included using a compound symmetry structure for the within-subject covariance matrix. Consistency of variance across groups was tested using Brown–Forsythe tests of homogeneity (Brown and Forsythe 1974) and any factors displaying heterogeneity were

modeled as dispersion effects. Denominator degrees of freedom for tests of fixed effects were calculated using general Satterthwaite approximations (Satterthwaite 1946). Tukey–Kramer multiple comparison tests of differences between least-squares means were performed for significant factors. Mann–Whitney tests were used to test for differences between live and dead animals of each species and age-class combination and Wilcoxon signed rank tests were used to examine differences in isotope ratios between mother-pup pairs and repeated samples from the same animal.

Relative FA concentrations are expressed as mass percent of total FAs and are designated according to the nomenclature of the International Union of Pure and Applied Chemistry (IUPAC) of carbon-chain-length:number-of-double-bonds and location of the double bond nearest the terminal methyl group (n-x). Relative FA concentrations were arcsine-square-root transformed prior to statistical treatment. Multivariate analysis of variance (MANOVA) was used to examine differences in FA profiles between species and years. Data from blubber samples collected in both years were examined simultaneously via Principal Component Analysis (PCA) using FAs present in amounts $\geq$0.5% in at least one species in one year. Since samples from each year were analyzed in separate labs using different methods, FA data were then examined via PCA for each year individually, using the set of FAs present for that particular year only. Since these multivariate techniques require that the number of samples in each group to be examined exceeds the number of variables, only FAs that occur on the extended dietary fatty acid list presented by Iverson *et al.* (2004) were used. Linear regression was used to examine the relationship between each principle component (PC) and $\delta^{13}C$ and $\delta^{15}N$ of vibrissae of

NFS and SSL from which both samples were taken. ANOVA was used to examine the equality of levels of saturated, monounsaturated, and polyunsaturated FAs between species and years. Tukey–Kramer multiple comparison tests of differences between means were performed for significant factors.

Differences in FA profiles between species for both years combined were also examined using a classification and regression tree (CART) analysis on the relative FA concentrations using the R package "rpart" (Therneau and Atkinson 2010). CART is a non-parametric data classification technique with fewer restrictions on sample size, number of variables, and normality of data than parametric methods. CART is an iterative technique that recursively partitions the data into groups that are as different as possible based on the variable that explains the largest amount of variation at each iteration. The set of 22 FAs that were quantified by both labs were used for the CART analysis.

All means are reported ± SEM. Statistical analyses were performed at the 95% significance level using SAS version 9.1 (SAS Institute Inc, Cary, North Carolina) and R version 2.11.1 (R Development Core Team 2010).

RESULTS

Stable isotopes

Mean nitrogen and carbon isotope values differed between species and age class (Figure 6). Ratios of stable nitrogen isotopes (Table 10) were significantly higher in SSL

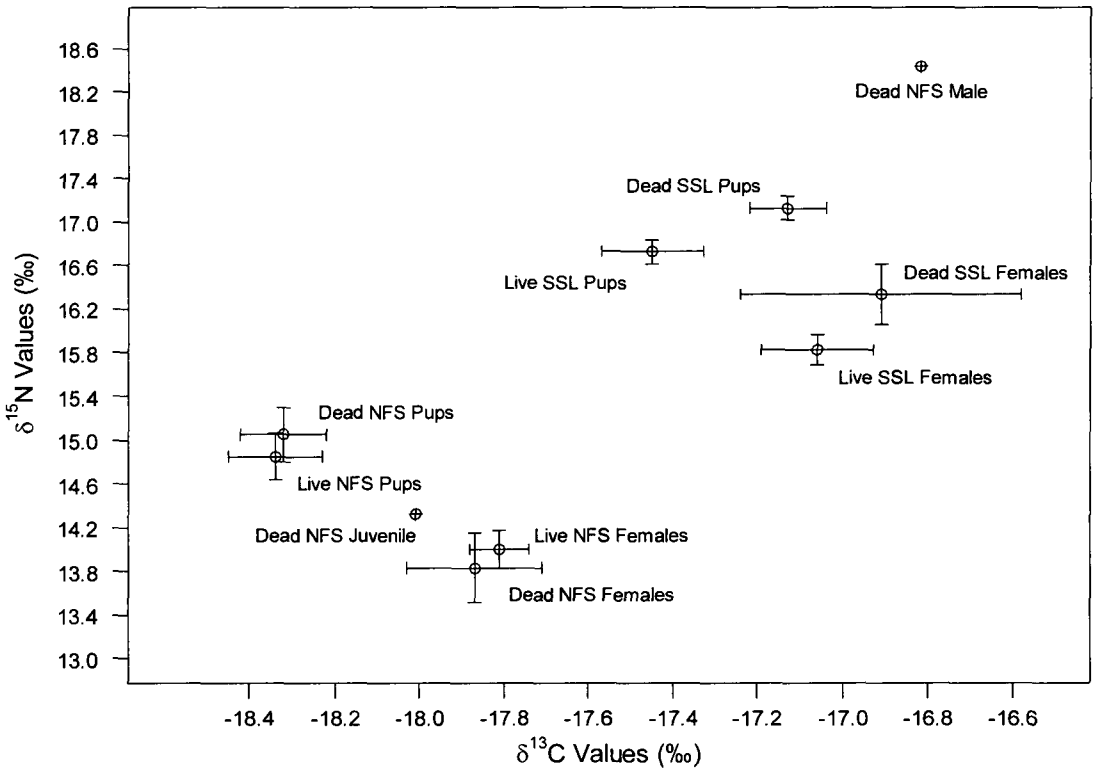

Figure 6. Mean (± SEM) $\delta^{15}N$ and $\delta^{13}C$ values for vibrissal roots of northern fur seals and Steller sea lions collected during the breeding seasons of 2007 and 2008 on Lovushki Island, Russia.

Table 10. Least-square mean (± SEM) $\delta^{15}N$ values for vibrissal roots of northern fur seals and Steller sea lions collected during the summer of 2007 and 2008 on Lovushki Island, Russia.

	2007		2008		Total	
	n	‰	*n*	‰	*n*	‰
Northern fur seals	**50**	**14.73 ± 0.13**	**45**	**14.07 ± 0.16**	**95**	**14.26 ± 0.11**
Adult females	31	14.09 ± 0.20	19	13.48 ± 0.26	50	13.91 ± 0.25
Live	26	14.36 ± 0.16	19	13.48 ± 0.26	45	14.31 ± 0.12
Dead	5	13.83 ± 0.36			5	13.83 ± 0.36
Pups	18	15.53 ± 0.19	25	14.51 ± 0.23	43	14.95 ± 0.17
Live	9	15.25 ± 0.16	14	14.59 ± 0.31	23	14.85 ± 0.23
Dead	9	15.81 ± 0.27	11	14.43 ± 0.35	20	15.05 ± 0.24
Adult male			1	18.43 ± 0.0	1	18.43 ± 0.0
Juveniles (unknown sex)	1	14.32 ± 0.0			1	14.32 ± 0.0
Steller sea lions	**17**	**16.59 ± 0.19**	**46**	**16.50 ± 0.16**	**63**	**16.57 ± 0.13**
Adult females	6	16.16 ± 0.21	22	16.06 ± 0.13	28	16.19 ± 0.13
Live	6	16.16 ± 0.21	13	15.77 ± 0.16	19	15.89 ± 0.14
Dead			9	16.35 ± 0.21	9	16.35 ± 0.21
Pups	11	17.13 ± 0.22	24	16.93 ± 0.12	35	16.93 ± 0.12
Live			11	16.73 ± 0.17	11	16.73 ± 0.17
Dead	11	17.13 ± 0.22	13	17.12 ± 0.16	24	17.13 ± 0.13

than in NFS (ANOVA: $F_{1, 129} = 176.42, p < 0.001$). Adult female SSL were enriched over adult female NFS by 2.15‰ ± 0.22‰ (ANOVA with Tukey–Kramer post-hoc test, $t_{74} = -9.63, p < 0.001$). The range in $\delta^{15}N$ values for SSL and NFS was 14.58‰ to 17.60‰ and 10.92‰ to 15.84‰, respectively. Pups, overall, had a significantly higher mean $\delta^{15}N$ value than adult females ($F_{2, 124} = 21.27, p < 0.001$). Nitrogen isotope values of NFS vibrissae in 2007 were enriched by 0.89‰ ± 0.18‰ over values in 2008 (Tukey–Kramer, $t_{154} = 4.91, p < 0.001$), but there was no difference between years for SSL ($p = 0.627$). There was no significant difference in mean $\delta^{15}N$ values between live and dead SSL and NFS ($p > 0.05$).

Mean stable carbon isotope values (Table 11) were also significantly higher in SSL than in NFS (ANOVA: $F_{1, 151} = 122.69, p < 0.001$). Adult female SSL were enriched over adult female NFS by 2.04‰ ± 0.23‰ (ANOVA with Tukey–Kramer post-hoc test, $t_{74} = -8.71, p < 0.001$). The range in $\delta^{13}C$ values for SSL and NFS was -15.44‰ to -17.93‰ and -16.94‰ to -19.19‰, respectively. Overall, NFS adult females were significantly enriched in $\delta^{13}C$ over NFS pups by 0.52‰ ± 0.11‰ (Tukey–Kramer, $t_{157} = 4.67, p < 0.001$) but there was not a significant difference between SSL pups and adult females. There was no significant difference in $\delta^{13}C$ levels between years or between live and dead SSL and NFS ($p > 0.05$).

Values of both isotope ratios differed between vibrissae collected from known pairs of mothers and pups (Table 12). NFS pups were significantly enriched in $\delta^{15}N$ over their mothers ($V = 9, p < 0.001$) and had significantly lower $\delta^{13}C$ values ($V = 216, p < 0.001$). SSL pups were also significantly enriched in $\delta^{15}N$ over their mothers ($V = 1, p =$

Table 11. Least-square mean (±SEM) $\delta^{13}C$ values for vibrissal roots of northern fur seals and Steller sea lions collected during the summer of 2007 and 2008 on Lovushki Island, Russia.

	2007		2008		Total	
	n	‰	*n*	‰	*n*	‰
Northern fur seals	**50**	-17.92 ± 0.08	**45**	-18.19 ± 0.08	**95**	-18.05 ± 0.06
Adult females	31	-17.76 ± 0.12	19	-18.03 ± 0.11	50	-17.88 ± 0.13
Live	26	-17.62 ± 0.10	19	-18.03 ± 0.11	45	-17.81 ± 0.08
Dead	5	-17.87 ± 0.18			5	-17.87 ± 0.18
Pups	18	-18.35 ± 0.12	25	-18.30 ± 0.10	43	-18.32 ± 0.08
Live	9	-18.27 ± 0.18	14	-18.38 ± 0.13	23	-18.34 ± 0.11
Dead	9	-18.44 ± 0.13	11	-18.22 ± 0.14	20	-18.31 ± 0.11
Males			1	-16.82 ± 0.00	1	-16.82 ± 0.00
Juveniles	1	-18.01 ± 0.00			1	-18.01 ± 0.00
Steller sea lions	**17**	-17.11 ± 0.12	**46**	-17.15 ± 0.08	**63**	-17.12 ± 0.07
Adult females	6	-17.18 ± 0.22	22	-16.94 ± 0.13	28	-16.93 ± 0.13
Live	6	-17.18 ± 0.22	13	-16.98 ± 0.16	19	-17.06 ± 0.13
Dead			9	-16.90 ± 0.21	9	-16.90 ± 0.21
Pups	11	-17.06 ± 0.20	24	-17.33 ± 0.12	35	-17.30 ± 0.11
Live			11	-17.47 ± 0.17	11	-17.47 ± 0.17
Dead	11	-17.06 ± 0.20	13	-17.19 ± 0.16	24	-17.13 ± 0.12

Table 12. $\delta^{15}N$ and $\delta^{13}C$ values of vibrissal roots from northern fur seal (NFS) and Steller sea lion (SSL) mother-pup pairs.

		$\delta^{15}N$ (‰)			$\delta^{13}C$ (‰)		
Animal ID	**Species**	**Mother**	**Pup**	$\Delta_{pup\text{-}mother}$	**Mother**	**Pup**	$\Delta_{pup\text{-}mother}$
NFS-07-16	NFS	15.00	15.46	0.46	-17.30	-18.07	-0.77
NFS-07-17	NFS	15.30	15.47	0.18	-17.99	-18.60	-0.61
NFS-07-18	NFS	15.29	15.31	0.02	-17.64	-18.23	-0.59
NFS-07-19	NFS	15.13	16.59	1.45	-17.33	-18.60	-1.27
NFS-07-21	NFS	12.99	14.00	1.01	-18.42	-19.28	-0.86
NFS-07-22	NFS	15.84	15.69	-0.15	-17.39	-17.79	-0.39
NFS-07-24	NFS	13.58	14.39	0.81	-17.76	-17.79	-0.03
NFS-07-25	NFS	14.72	14.90	0.18	-17.46	-17.84	-0.38
NFS-07-27	NFS	15.81	15.44	-0.37	-17.56	-18.20	-0.64
NFS-08-02	NFS	13.17	15.10	1.93	-17.65	-18.08	-0.43
NFS-08-04	NFS	13.81	15.51	1.70	-18.40	-18.43	-0.03
NFS-08-05	NFS	12.22	13.51	1.29	-18.50	-19.29	-0.79
NFS-08-06	NFS	13.29	14.76	1.47	-17.88	-17.93	-0.05
NFS-08-08	NFS	13.56	14.89	1.33	-17.71	-17.93	-0.22
NFS-08-09	NFS	14.40	15.44	1.04	-17.76	-18.16	-0.39
NFS-08-10	NFS	10.92	14.53	3.61	-18.57	-17.94	0.63
NFS-08-11	NFS	13.59	14.31	0.71	-17.48	-17.90	-0.43
NFS-08-12	NFS	13.19	14.81	1.62	-17.88	-18.08	-0.20
NFS-08-13	NFS	13.23	14.67	1.44	-18.19	-18.45	-0.26
NFS-08-14	NFS	12.55	12.61	0.06	-18.44	-19.21	-0.76
NFS-08-15	NFS	15.53	16.29	0.76	-18.08	-18.50	-0.42
SSL-08-01	SSL	14.95	16.43	1.48	-17.50	-17.82	-0.32
SSL-08-02	SSL	16.68	16.55	-0.13	-15.71	-17.36	-1.65
SSL-08-05	SSL	16.03	16.56	0.53	-17.31	-17.77	-0.47
SSL-08-11	SSL	15.18	17.21	2.02	-16.36	-16.72	-0.36
SSL-08-12	SSL	15.67	17.16	1.50	-17.56	-17.33	0.24
SSL-08-13	SSL	15.76	17.34	1.59	-16.76	-16.81	-0.05

0.031) and had significantly lower $\delta^{13}C$ values ($V = 19$, $p = 0.047$). The mean nitrogen enrichment of pups over their mothers was 0.98‰ ± 0.20‰ (range -0.37‰ to 3.61‰) for NFS and 1.16‰ ± 0.33‰ (range -0.13‰ to 2.02‰) for SSL. The mean depletion of carbon was 0.42‰ ± 0.09‰ (range -0.63‰ to 1.26‰) for NFS pups and 0.44‰ ± 0.26‰ (range -0.13‰ to 2.02‰) for SSL pups. However, not all mother-pup pairs followed this pattern. Of the 21 NFS pairs, two (9.5%) of the pups had lower $\delta^{15}N$ values than their mothers and one (4.8%) had a higher $\delta^{13}C$ value than its mother. Of the six SSL pairs, one (16.7%) had a lower $\delta^{15}N$ value and one had a higher $\delta^{13}C$ value than its mother.

Isotopic values from repeated samplings of the same animal were not significantly different (Table 13). Mean $\delta^{15}N$ values of NFS ($n = 2$) and SSL ($n = 4$) vibrissae sampled later in the breeding season were 0.38‰ ± 0.08‰ and 0.50‰ ± 0.75‰ higher than vibrissae sampled from the same animal sampled earlier in the breeding season, respectively. Mean $\delta^{13}C$ values of vibrissae sampled from NFS and SSL later in the breeding season were 1.07‰ ± 0.26‰ and 0.51‰ ± 0.56‰ lower than vibrissae sampled from the same animal earlier in the breeding season, respectively. Although these differences were not significant, sample sizes may be too small to make any strong statistical inferences.

Fatty acids

A total of 60 and 54 FAs were identified in greater than trace amounts (≥0.5%) in samples from both NFS and SSL, respectively, collected in 2007 and 2008. Of these, a

Table 13. Change in $\delta^{15}N$ and $\delta^{13}C$ values over time for repeated samplings of vibrissal roots from recaptured northern fur seals and Steller sea lions.

			$\delta^{15}N$ (‰)			$\delta^{13}C$ (‰)		
Animal ID	**Species**	Δ_{days}	**Time 1**	**Time 2**	Δ_{2-1}	**Time 1**	**Time 2**	Δ_{2-1}
NFS-07-03	NFS	8	14.52	14.82	0.30	-17.54	-18.35	-0.80
NFS-07-06	NFS	39	14.47	14.92	0.45	-16.92	-18.25	-1.33
SSL-07-01	SSL	12	15.86	16.88	1.02	-18.20	-17.65	0.55
SSL-07-03	SSL	8	17.37	15.64	-1.73	-15.52	-17.60	-2.08
SSL-07-04	SSL	8	15.06	16.21	1.15	-17.45	-17.61	-0.16
SSL-07-05	SSL	8	16.18	17.74	1.56	-16.18	-16.51	-0.33

common set of 22 FAs were quantified in both years by both labs (Table 14). In both years, the major saturated fatty acids (SFA) found in both NFS and SSL blubber samples were 14:0 and 16:0 and the major monounsaturated fatty acids (MUFA) were 18:1n-9 and 20:1. In 2007, SSL blubber samples also contained higher levels of 16:1 than in 2008. In 2007, the major polyunsaturated fatty acid (PUFA) was 22:6n-3, and in 2008 the major PUFA were 18:2n-6, 22:2, 20:5n-3, and 22:6n-3. There was a significant difference in overall levels of SFA ($F_{2,53} = 109.2, p < 0.005$), MUFA ($F_{2,53} = 42.81, p < 0.005$), and PUFA ($F_{2,53} = 166.34, p < 0.005$) in both species between years (Figure 7). NFS blubber contained significantly higher levels of SFA than SSL in 2007 ($t_{1,53} = 2.94, p < 0.005$, Tukey post-hoc test) and significantly lower levels in 2008 ($t_{1,53} = -4.07, p < 0.005$). There were no significant differences in overall levels of MUFA between species in either year, nor was there a significant difference in overall levels of PUFA between species in 2007. However, NFS blubber from 2008 contained significantly higher overall levels of PUFA compared to SSL samples ($t_{1,53} = 2.51, p = 0.015$).

FA profiles were significantly different between species (MANOVA: $F_{16,38} = 28.77, p < 0.001$) and between years ($F_{16,38} = 430.37, p < 0.001$) with a significant species by year interaction ($F_{16,38} = 39.32, p < 0.001$). Of these FAs, 12 showed significant differences between species (MANOVA, test of between-subject effects, $p < 0.05$ in each case), 14 showed significant differences between years ($p < 0.05$ in each case), and 5 showed significant species by year interaction ($p < 0.05$ in each case).

Table 14. Mean relative concentration (±SEM) of the 22 fatty acids quantified in northern fur seal (NFS) and Steller sea lion (SSL) blubber from 2007 and 2008. SFA: saturated fatty acids; MUFA: mono-unsaturated fatty acids; PUFA poly-unsaturated fatty acids.

	2007		2008	
	NFS	**SSL**	**NFS**	**SSL**
Fatty Acid	$n = 26$	$n = 6$	$n = 15$	$n = 10$
14:0	6.54 ± 0.26	8.68 ± 0.26	3.20 ± 0.22	4.47 ± 1.52
16:0	18.78 ± 0.61	16.65 ± 0.99	9.76 ± 0.54	6.49 ± 1.89
18:0	6.24 ± 0.22	2.33 ± 0.11	1.20 ± 0.14	6.56 ± 1.96
20:0	0.43 ± 0.03	0.17 ± 0.01	2.46 ± 0.22	2.78 ± 0.73
22:0	0.04 ± 0.01	0.0 ± 0.0	0.94 ± 0.16	2.27 ± 0.66
SFA	**32.04 ± 0.53**	**27.82 ± 1.23**	**17.55 ± 0.57**	**22.57 ± 1.50**
14:1	0.15 ± 0.02	0.93 ± 0.01	0.50 ± 0.04	0.27 ± 0.13
15:1	–	–	0.18 ± 0.06	1.47 ± 0.42
16:1	4.37 ± 0.34	15.54 ± 0.62	3.93 ± 0.34	2.17 ± 0.58
18:1n-9	34.38 ± 0.54	31.22 ± 0.60	16.61 ± 2.08	25.68 ± 4.13
20:1	12.04 ± 0.59	8.06 ± 0.42	9.80 ± 0.67	4.62 ± 1.46
22:1n-9	1.96 ± 0.14	1.50 ± 0.10	0.41 ± 0.11	0.32 ± 0.12
24:1	0.57 ± 0.05	0.40 ± 0.01	2.92 ± 0.96	1.25 ± 0.28
MUFA	**53.47 ± 0.78**	**57.65 ± 0.55**	**34.35 ± 2.27**	**35.77 ± 4.45**
18:2n-6	1.63 ± 0.05	1.72 ± 0.16	12.77 ± 0.36	14.32 ± 1.53
18:3n-6	0.13 ± 0.01	0.05 ± 0.02	3.50 ± 0.39	1.91 ± 0.38
18:3n-3	0.55 ± 0.04	0.53 ± 0.03	0.01 ± 0.00	–
20:2	0.53 ± 0.02	0.24 ± 0.02	1.58 ± 0.23	0.71 ± 0.24
20:3n-3	0.22 ± 0.01	0.08 ± 0.01	1.99 ± 0.39	1.10 ± 0.23
20:3n-6	0.15 ± 0.01	0.11 ± 0.01	2.95 ± 0.25	3.09 ± 0.81
20:4n-6	0.50 ± 0.04	0.41 ± 0.05	0.88 ± 0.21	1.92 ± 0.98
20:5n-3	1.99 ± 0.26	4.32 ± 0.33	0.67 ± 0.25	10.54 ± 2.25
22:2	–	–	11.40 ± 1.31	0.34 ± 0.29
22:6n-3	8.75 ± 0.52	6.94 ± 0.76	12.32 ± 0.64	7.58 ± 2.37
PUFA	**14.45 ± 0.68**	**14.41 ± 1.01**	**48.06 ± 1.92**	**41.52 ± 3.41**

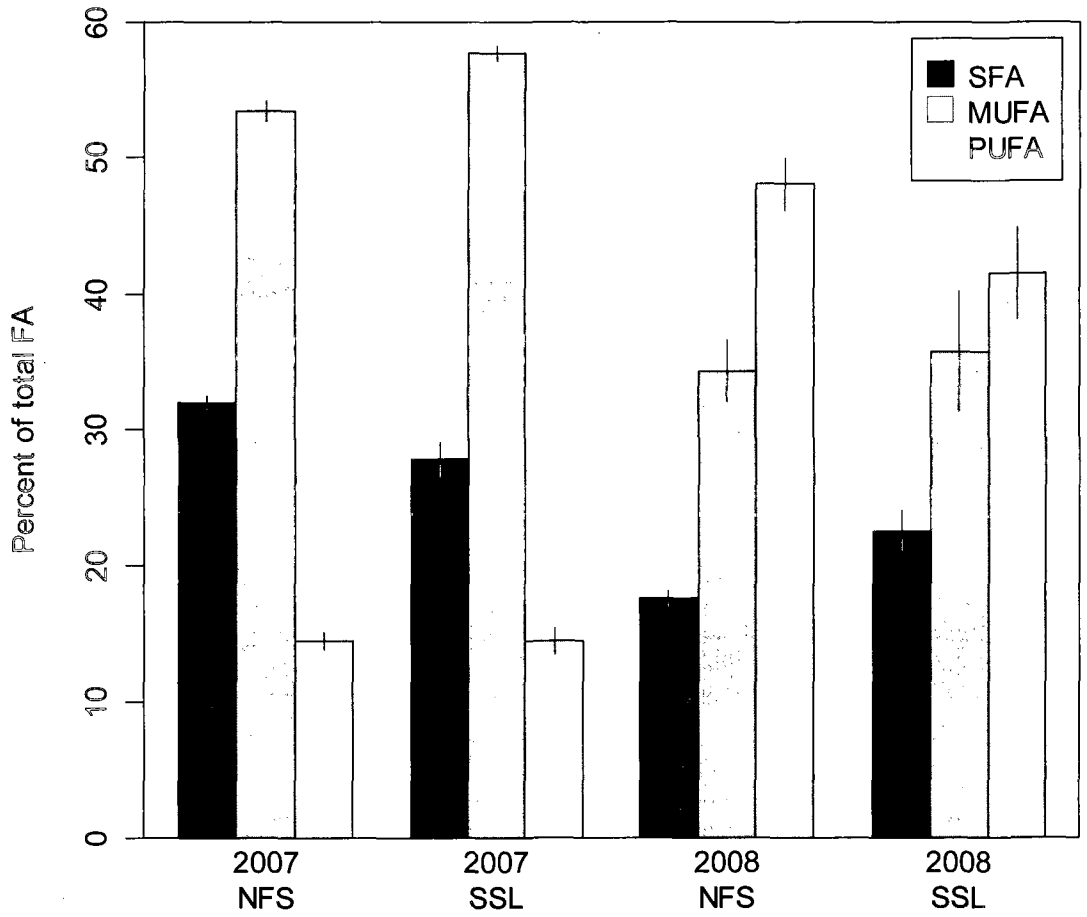

Figure 7. Relative concentrations of saturated (SFA), monounsaturated (MUFA), and polyunsaturated (PUFA) fatty acids found in northern fur seal (NFS) and Steller sea lion (SSL) blubber in 2007 and 2008. Error bars are ± SEM.

The same set of 16 FAs that was used in the MANOVA was used in the PCA analysis for the combined years. The first 2 principle components (PC) in the analysis of all samples accounted for 74.9% of the total variance in the FA profiles. PC1 clearly separated the two years and, although not as strongly, the two species within each year. PC1 represented a gradient from samples containing higher relative levels of 18:2n6, 18:3n3, and 20:3n-6 to samples higher in 18:1n-9, 22:1n-9, and 18:3n-3. PC2 separated the predator species within each year and represented a gradient from samples with higher concentrations of 20:5n-3, 22:0, and 18:1n-9 to samples higher in 20:1, 20:4n-6, and 22:6n-3 (Figure 8, Table 15).

For samples collected in 2007, 11 FAs were used in the PCA. The first 3 PCs in this analysis accounted for 84.6% of the total variance in FA profiles. PC1 and PC3 each separated the predator groups, while PC2 did not (Figure 9). Samples along PC1 represented a gradient from higher concentrations of 20:5n-3, 16:1, and 18:3n-3 to samples with higher concentrations of 20:1, 22:1n-9, and 20:2. Samples along PC2 represented a gradient from higher concentrations of 16:0, 20:1n-9, and 16:1 to samples with higher concentrations of 22:6n-3, 18:2n-6, and 20:4n-3. PC3 represented a gradient from higher concentrations of 16:0, 20:4n-6, and 18:1n-9 to samples with higher concentrations of 18:2n-6, 16:1, and 22:1n-9.

For samples collected in 2008, 14 FAs were used in the PCA and the first 3 PCs accounted for 76.6% of the total variance. PC1 separated the samples into 3 distinct groups: NFS, SSL sampled in June, and SSL sampled in July by remote biopsy (Figure 9). With the exception of one SSL, PC2 clearly separated the predator species, while PC3

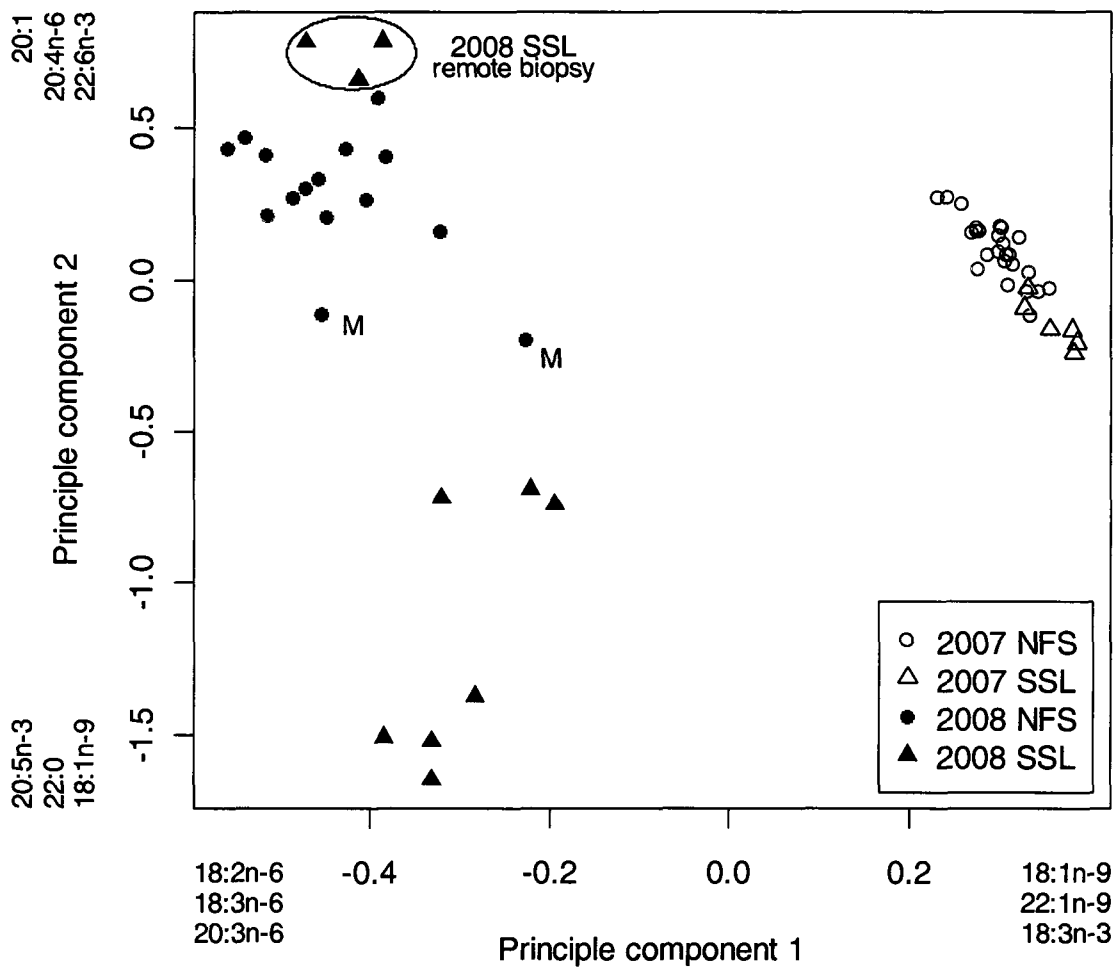

Figure 8. Plot of PC1 and PC2 from principle components analysis on fatty acid composition of blubber of northern fur seals (NFS, circles) and Steller sea lions (SSL, triangles) collected in 2007 (open shapes) and 2008 (filled shapes). Two male NFS are indicated by the letter "M"

Table 15. Loadings from principle component analyses of fatty acid profiles from northern fur seals and Steller sea lions. Fatty acids with a loading value of 0 indicate a variable that was not used in that particular analysis.

Fatty	Combined years			2007			2008		
Acid	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
16:0	0.261	0.303	0.082	-0.258	-0.202	-0.460	0.361	0.035	-0.047
22:0	-0.264	-0.313	-0.105	0	0	0	-0.332	-0.088	-0.076
16:1	0.163	-0.021	0.032	-0.366	-0.074	0.341	0.038	-0.444	0.237
18:1n-9	0.269	-0.272	-0.132	0.252	-0.186	-0.377	-0.340	-0.028	-0.078
20:1	0.138	0.326	-0.475	0.400	-0.052	-0.122	0.256	-0.312	0.400
22:1n-9	0.279	0.196	-0.094	0.355	0.018	0.263	0	0	0
18:2n-6	-0.348	-0.009	0.158	0.130	0.477	0.351	0.177	0.411	-0.126
18:3n-6	-0.335	0.092	-0.056	-0.285	0.352	-0.249	0.251	-0.232	-0.321
18:3n-3	0.336	0.059	0.042	0	0	0	0	0	0
20:2	-0.213	0.137	-0.508	0.352	0.247	-0.313	0.127	-0.396	-0.046
20:3n-3	-0.290	-0.067	-0.161	0	0	0	-0.044	-0.305	-0.727
20:3n-6	-0.326	0.118	0.192	0	0	0	0.292	0.231	0.157
20:4n-6	-0.065	0.329	0.561	-0.256	0.361	-0.386	0.271	0.305	-0.278
20:5n-3	0.024	-0.439	0.162	-0.399	0.025	0.119	-0.340	0.084	0.132
22:2	-0.264	0.207	-0.168	0	0	0	0.234	-0.261	0.010
22:6n-3	*-0.096*	*0.445*	*0.094*	*0.059*	*0.610*	*-0.024*	*0.368*	*0.019*	*0.007*

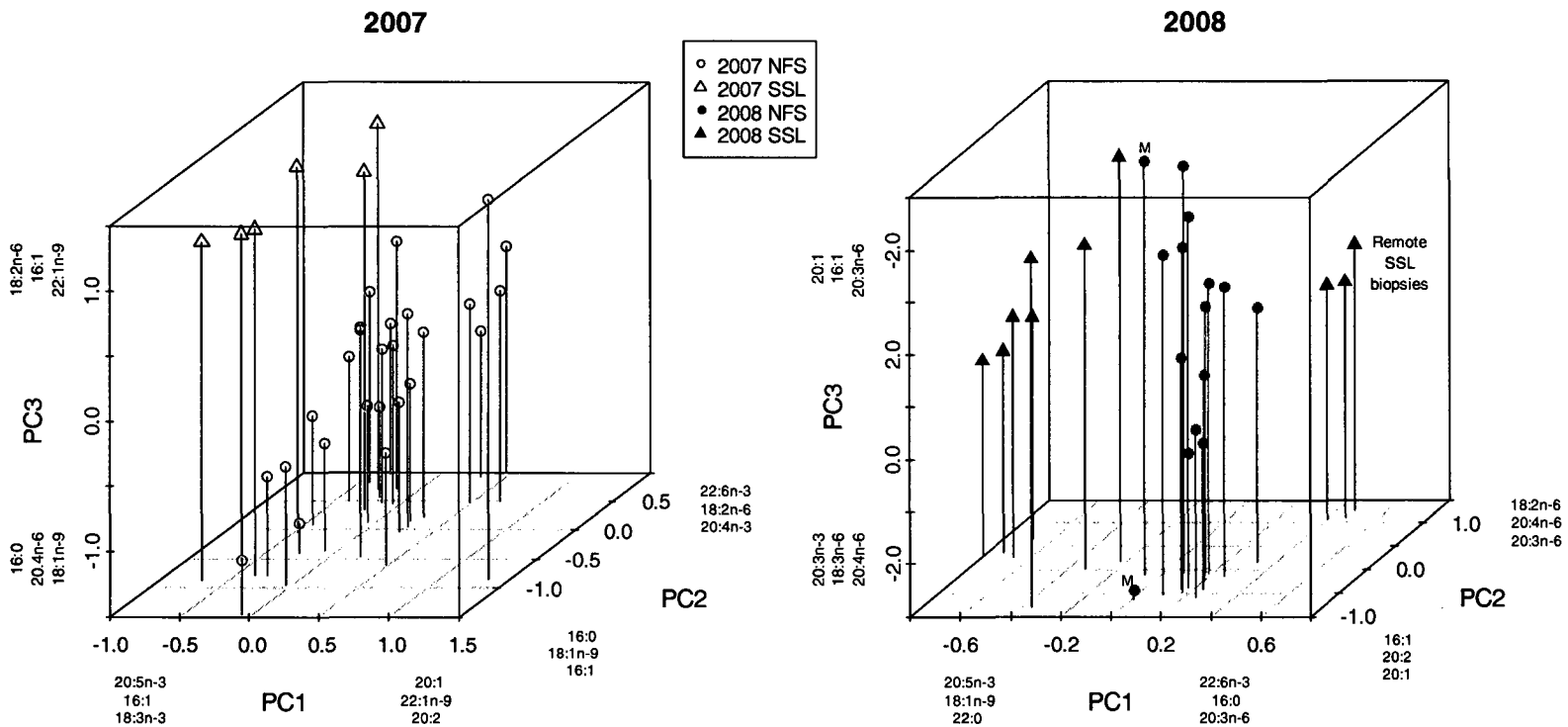

Figure 9. Plot of PC1, PC2, and PC3 from principle components analysis on fatty acid composition of blubber of northern fur seals (NFS, circles) and Steller sea lions (SSL, triangles) collected in 2007 and 2008. Two male NFS are indicated by the letter "M"

did not. PC1 represented a gradient from samples with higher concentrations of 20:5n-3, 18:1n-9, and 22:0 to samples higher in 22:6n-3, 16:0, and 20:3n-6. PC2 represented a gradient from samples enriched in 16:1, 20:2, and 20:1 to samples with higher concentrations of 18:2n-6, 20:4n-6, and 20:3n-6. PC3 represented a gradient from samples enriched in 20:3n-3, 18:3n6, and 20:4n-6 to samples with higher concentrations of 20:1, 16:1, and 20:3n-6.

Both PC2 and PC3 from the combined-year PCA were significant predictors of foraging location (PC2: $F_{1,48} = 20.52, p < 0.005$; PC3: $F_{1,48} = 6.18, p = 0.016$) and trophic level (PC2: $F_{1,48} = 10.80, p = 0.002$; PC3: $F_{1,48} = 11.78, p = 0.001$) based on $\delta^{13}C$ and $\delta^{15}N$ levels of vibrissae, respectively. PC3 from the 2007 PCA was a significant predictor of trophic level ($F_{1,29} = 13.70, p < 0.001$), but none of the principle components were significant predictors of foraging location. Both PC1 and PC2 from the 2008 PCA were significant predictors of both trophic level (PC1: $F_{1,17} = 10.18, p = 0.005$; PC2: $F_{1,17} = 5.42, p = 0.032$) and foraging location (PC1: $F_{1,17} = 20.47, p < 0.005$; PC2: $F_{1,17} = 6.03, p = 0.025$).

CART analysis of FA profiles of NFS and SSL from both 2007 and 2008 correctly classified 94.7% of the samples (38 of 41 NFS and 16 of 16 SSL). At the first branch, 68.8% of the SSL were separated from the remaining samples based on elevated levels of 20:5n-3 (Figure 10). The remaining SSL samples, along with 7.3% ($n = 3$) of the NFS samples, were separated at the next branch based on elevated 14:0. Of these SSL samples, 60% were the three samples taken in late July of 2008 by remote biopsy. The

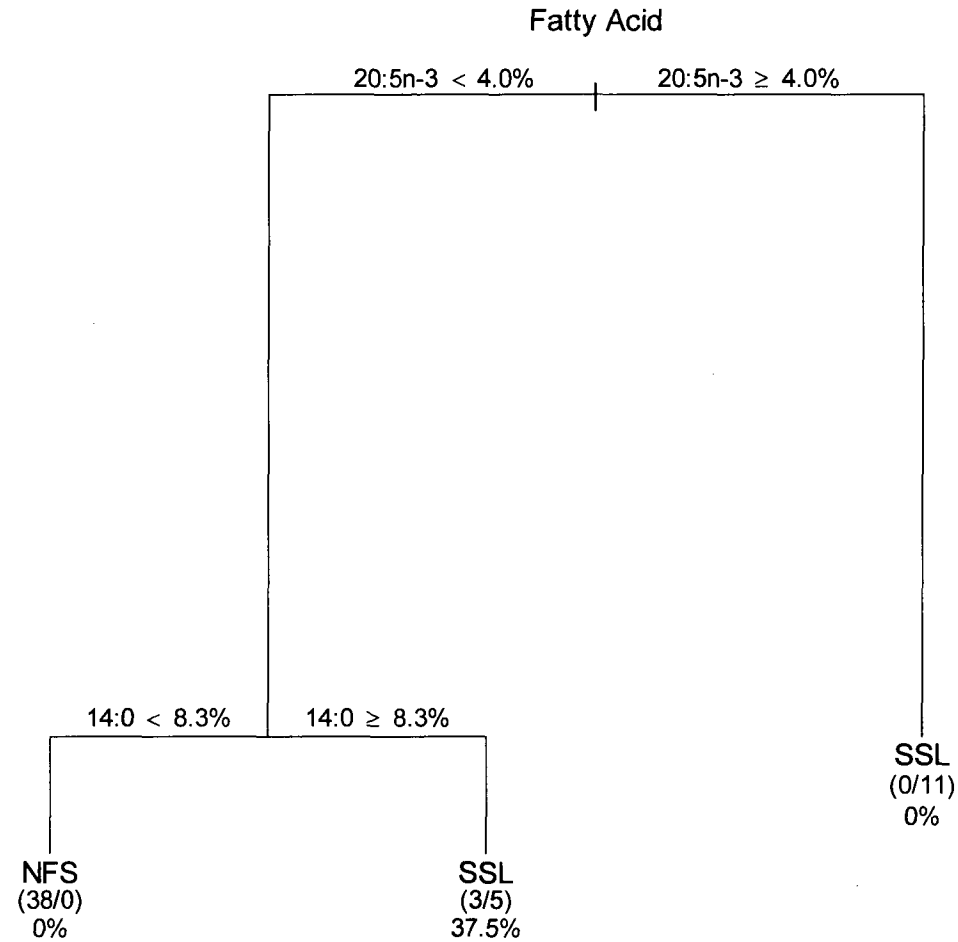

Figure 10. Results of classification and regression tree analysis on the fatty acid composition of northern fur seal (NFS) and Steller sea lion (SSL) blubber samples. Labels at each branch represent the classification rules. Labels at the terminal nodes denote the expected species classification, the number of NFS/SSL in each node, and the misclassification rate.

remaining two samples were collected in June of 2007. The majority of NFS samples (92.7%) were all classified based on lower 20:5n-3 and 14:0 concentrations.

DISCUSSION

Stable isotopes

Stable isotope analysis of vibrissal roots indicates that adult female SSL and NFS on Lovushki Island partition the available foraging resources, thus reducing the amount of inter-specific competition and allowing the breeding populations of both predator species to coexist despite the rapid increase in the NFS population. Mean levels of $\delta^{15}N$ indicate that adult female SSL on Lovushki Island fed at a higher trophic level than adult female NFS and the mean $\delta^{13}C$ values suggest that the two species foraged in different locations. Based on stable carbon isotope levels, the SSL in this study foraged nearshore and/or benthically while the NFS fed offshore and pelagically. Hobson *et al.* (1997) found similar results for the $\delta^{15}N$ levels of NFS and SSL samples collected in the Pribilof Islands and Gulf of Alaska, respectively. The same study found no significant difference in $\delta^{13}C$ values, though this could be accounted for by the different geographical locations in which the samples were collected.

The physiological state of an animal, including nutritional stress due to fasting, pregnancy, or lactation, can affect the interpretation of $\delta^{15}N$ values (Kurle and Worthy 2001, Fuller *et al.* 2004). During the breeding season, adult female SSL and NFS with

dependent pups undergo episodic fasts while nursing their young onshore and their level of nutritional stress is difficult to assess, and therefore, the use of nitrogen SI to determine specific prey may not be possible. Nutritional stress has been found to have no effect on ^{13}C enrichment in animal tissues (Teeri and Schoeller 1979, Hobson *et al.* 1993, Kempster *et al.* 2007) therefore, based on analyses of stable nitrogen and carbon isotopes, we can only make general inferences on the specific diet of SSL and NFS using known fish distributions from trawl surveys and diet studies of pinnipeds on Lovushki Island and nearby rookeries, as well as the relative trophic positions of the potential prey items themselves.

Analysis of undigested prey remains recovered from scats and spews collected on Lovushki Island during the breeding seasons of 2007 and 2008 showed that breeding female SSL and NFS had significantly different diets from one another (Chapter 1). Based on percent numerical abundance, SSL fed almost exclusively on Atka mackerel (*Pleurogrammus monopterygius*) while NFS feed primarily on northern smoothtongue (*Leuroglossus schmidti)* and squid (*Gonatopsis* sp.). Although potential biases associated with scat analysis require these results to be interpreted with some caution, these results support the stable isotope data presented in this paper from the standpoint of the relative trophic positions of the prey items, as well as their general distribution and preferred habitat.

Ratios of nitrogen SI indicate the relative trophic position of an organism in the food chain. Atka mackerel, the primary summer prey of SSL on Lovushki Island, found in the Russian Far East have an estimated trophic level of 3.3–3.9 (Brodeur and

Livingston 1988, Zolotov and Tokranov 1991, Onishchick 1997). In contrast, the primary prey of breeding NFS on Lovushki Island have relatively lower estimated trophic levels: northern smoothtongue from the Bering Sea have an estimated trophic level of 3.1–3.2 (Gorbatenko and Il'inskii 1992, Balanov *et al.* 1994) and Gonatid squids range from 3.2–3.4 (Pauly *et al.* 1998, Gorbatenko *et al.* 2008). Using published data on stomach contents, Pauly *et al.* (1998) estimated the trophic position of both NFS and SSL as 4.2. However, based on the diet estimates derived from scat data and the trophic positions of the prey, it would be expected for breeding female SSL on Lovushki Island to be at a relative higher trophic level than breeding female NFS. This expectation coincides with the higher mean $\delta^{15}N$ levels of the vibrissal roots from SSL examined in this study.

Similarly, foraging location inferred from mean $\delta^{13}C$ levels of vibrissal roots coincide with the distribution and habitat of prey items identified from scats and spews. The general trend in $\delta^{13}C$ enrichment in organisms is an increase moving from offshore and pelagic to nearshore and benthic. During the summer spawning season, Atka mackerel are demersal and spawn in nearshore, shallow waters, living at depths ranging from the inter-tidal zone to <200 m (Gorbunova 1962, McDermott and Lowe 1997). Northern smoothtongue and accessible squid species are mid-water shelf and mesopelagic prey items, usually located farther offshore, and thus would generally be expected to have relatively lower $\delta^{13}C$ levels compared to Atka mackerel.

Mean $\delta^{15}N$ and $\delta^{13}C$ values for Atka mackerel collected from nearby waters (n = 2) was 12.4 ± 0.1‰ and -20.3 ± 0.1‰, respectively, for lipid-free tissue and 10.3 ± 0.7‰ and -21.4 ± 0.2‰, respectively, for squid beaks (n = 3) recovered from NFS stomachs (J.

Waite, unpub. data). Cherel and Hobson (2005) found that the lower beaks of Antarctic squid (*Psychroteuthis glacialis*) were enriched in $\delta^{13}C$ by 1.4 ± 0.5‰ (SD) and impoverished in $\delta^{15}N$ by 2.7 ± 0.4‰ compared to the buccal masses. The application of these correction factors to our Gonatid squid beaks results in estimated $\delta^{15}N$ and $\delta^{13}C$ values for tissue of approximately 13.0‰ and -22.1‰, respectively. The lower $\delta^{13}C$ values of the squid compared to the Atka mackerel coincide with both the expected habitats of these prey items as well as the lower $\delta^{13}C$ values of the NFS vibrissal roots compared to SSL. The $\delta^{15}N$ values of both prey items are comparable, which possibly reflects the overlap in their estimated trophic position. There are no published data on the stable isotope ratios of northern smoothtongue from nearby waters, but based on their estimated trophic position and mesopelagic habitat, we would expect $\delta^{13}C$ values similar to squid and $\delta^{15}N$ values lower than both Atka mackerel and squid. Both would coincide with the lower $\delta^{13}C$ and $\delta^{15}N$ levels found in the vibrissal roots of breeding NFS.

There was a significant increase in $\delta^{15}N$ levels in breeding NFS from 2007 to 2008. Although significance was not tested due to limitations of sample size, scat and spew data indicate a substantial increase in the consumption of cephalopods by breeding NFS from 16.2% (percent numerical abundance) in 2007 to 48.6% in 2008. There was a concurrent decrease in the consumption of northern smoothtongue from 47.9% to 30.9% (Chapter 1). This change in the scat-derived diet estimate would explain the different isotopic values found in this study and further support the convergence of the stable isotope and scat data.

SI ratios from repeated sampling of the same animals did not change significantly over a period of 4–6 weeks, indicating that either these animals did not alter their foraging strategies over the course of a substantial portion of the breeding season, or that the isotopic turnover rate in the vibrissal roots was longer than the amount of time that had elapsed between sample collections. Although this may suggest that a single, determined scat collection effort may accurately reflect diet over the course of the entire breeding season, the number of repeated vibrissae samplings was extremely small. This assertion could be tested by increasing the sample size of repeatedly-sampled animals and comparing the results with those of scat samples collected over the course of the entire breeding season.

Pups of both species fed at a higher trophic level than adults. The enrichment of $\delta^{15}N$ in NFS and SSL pups over adults from mother-pup pairs was less than a trophic level: 0.98‰ and 1.17‰, respectively. These results are similar to findings by Jenkins *et al.* (2001), where in a study of 11 different species of mammals, it was found that offspring plasma had a mean $\delta^{15}N$ enrichment of 0.9‰ ± 0.8‰ over maternal plasma. Jenkins *et al.* (2001) postulated that the enrichment in $\delta^{15}N$ of a complete trophic level likely did not occur due to depletion in $\delta^{15}N$ in milk relative to maternal plasma. The same study found no enrichment in $\delta^{13}C$ between pup and maternal plasma; however, our study found a significant depletion of $\delta^{13}C$ in NFS and SSL pup vibrissae by 0.42‰ and 0.44‰, respectively. This may be due to the higher lipid content of milk in NFS and SSL compared to the multiple species used in the Jenkins *et al.* (2001) study, as lipids are depleted in $\delta^{13}C$ relative to maternal plasma and other tissues.

Fatty acids

Differences in the relative composition of FAs in the blubber indicate that adult female NFS and SSL on Lovushki Island partition the available foraging resources through differences in either the prey species selected or in the proportion of different prey items consumed. It is generally not possible to determine predator diet based solely on the relative concentration of FAs. However, fish and cephalopods have a species-specific combination of FAs, and while within-species variation exists due to differences in geographical location, age, size, and time of year, this variation is typically less than the between-species variation (Budge *et al.* 2002, Iverson *et al.* 2002). Thus, while a reference library of prey FAs specific to this particular study location is not currently available, qualitative inferences may be made based on differences in the FA profile of prey types collected in other geographic regions within a similar time period.

A common theme in the PCA and CART analyses was the separation of species based on levels of 20:5n-3, which was significantly higher in SSL samples than in NFS samples. Although 20:5n-3 tends to occur at relatively high concentrations in most fish and squid species, northern smoothtongue is at the lower end of the spectrum (Iverson *et al.*, unpubl. data), while hexagrammids are towards the upper end (Iverson *et al.* 2002). Cephalopods (primarily squid) were the second most common NFS prey item identified in scats and spews. Cephalopod species can vary greatly in levels of 18:1n-9, ranging from 3.32 to 13.96% (Iverson *et al.* 2002, Stowasser *et al.* 2006), with most species having relatively high levels of 20:5n3 (Iverson *et al.* 2002). Though NFS samples

contained low levels of 18:1n-9, the low levels of 20:5n-3 contrasts with the FA composition of most squid species. However, squid species tend to have relatively low lipid content and it is unclear how much their FA profile would affect the FA composition of NFS blubber in comparison to northern smoothtongue, which has substantially higher lipid content. Furthermore, scat data indicate an increase in squid consumption and a concurrent decrease in northern smoothtongue consumption by NFS between 2007 and 2008, which is also supported by changes in stable nitrogen isotopes. However, NFS FA profiles showed a significant decrease in the levels of 20:5n-3 between 2007 and 2008 (ANOVA with Tukey–Kramer post-hoc test, $t_{53} = 2.66, p = 0.049$) as well as a significant increase in 18:1n-9 ($t_{53} = 7.55, p < 0.001$), which is not necessarily consistent with what would be expected based on the relative concentration of these two FAs in squid and northern smoothtongue. However, FA profiles of blubber from lactating female pinnipeds may also be affected by the selective mobilization of certain fatty acids from the blubber store for milk synthesis. Grahl-Nielsen *et al.* (2000) found that the milk of grey seals (*Halichoerus grypus*) was significantly enriched in most of the polyunsaturated n-3 FAs (such as 20:5n-3) and depleted in monounsaturated FAs with 18 carbon atoms (such as 18:1n-9). Iverson *et al.* (1995) also found that the milk of hooded seals (*Cystophora cristata*) contained consistently higher levels of 20:5n-3 than blubber. Therefore, the observed decrease in 20:5n-3 and increase in 18:1n-9 between 2007 and 2008 in NFS blubber samples may be consistent with an increase in squid consumption. This highlights some of the problems associated with using only a few FAs

when estimating dietary intake of predators, especially when the prey items being compared were collected in entirely different geographical regions.

As with SI data, without a reference library specific to the prey items in this particular region, the FA data may be best used to make inferences on trophic level and foraging location rather than to determine the specific prey species consumed. While PC1 from the combined-years PCA primarily separated samples by year, PC2 and PC3 were both significantly correlated with $\delta^{13}C$ and $\delta^{15}N$ levels of vibrissae. For example, PC2 represents a gradient from nearshore and benthic foraging to offshore and pelagic foraging and from higher to lower trophic level feeding.

Among the SSL sampled, the three individuals that were remotely biopsied later in the breeding season showed substantial differences in their FA profile. Principle component analysis indicates that these samples consisted of higher levels of 20:1, 20:4n-6, and 20:6n-3 and lower levels of 20:5n-3, 22:0, and 18:1n-9 compared to all other SSL samples from either year and more closely resemble NFS samples than they do other SSL samples. CART analysis initially separated these three samples, along with all of the NFS samples, from the remaining SSL samples based on lower levels of 20:5n-3, further supporting their resemblance to NFS samples. In addition to sampling method, these samples differed from the others by sampling location, sample mass, and time of year in which they were collected. Moreover, it is unknown whether the two remotely biopsied females had dependent pups on the rookery, as they were sampled while swimming near the support vessel.

The remote biopsies were taken approximately 30 days later than the direct biopsies and the different FA composition may reflect a temporal dietary change. By mid- to late-July, pups born to these two females should be fairly large and better able to sustain longer periods of fasting, allowing their mothers to forage for longer durations. As the trip duration increases, the foraging location may move farther away from the rookery where the SSL would encounter the same prey items consumed by adult female NFS, such as salmon, northern smoothtongue, and squid. If this pattern is common among SSL, the amount of inter-specific competition for prey resources would increase, specifically during the time when NFS are provisioning their newborn. This possibility could be explored through the examination of scats and vibrissae collected specifically during this later time period, though the available samples from this study are limited. However, pinnipeds may preferentially deposit and mobilize certain FAs during lactation (Wheatley *et al.* 2008) and the difference in the FA profile may have been due to a change in physiological requirements of these two female SSL or their pups.

The FA composition of the metabolically active blubber stores is relatively homogenous across the trunk of the body (Cooper 2004), thus the difference in sampling location alone is unlikely to explain the difference in the FA profiles seen in these three animals. However, though not as strongly as in cetaceans, the blubber of pinnipeds is stratified with respect to FA deposition, with the inner and outer portions representing more and less recent diets, respectively (Best *et al.* 2003, Iverson *et al.* 2004, Budge *et al.* 2006). The remotely collected SSL samples were significantly smaller (56.7 ± 9.6 mg, Mann–Whitney $U = 21, p = 0.017$) than samples collected directly in the same year

(174.0 ± 29.7 mg). As the diameter of the biopsy punches used for SSL in both methods was the same (6 mm), the smaller sample mass may be due to incomplete penetration of the remote biopsy tip, thereby collecting a sample more representative of the outer blubber layer. Thus, depending on the sampling depth and the amount of stratification in the blubber, these samples could represent either prey consumed prior to the breeding season when foraging strategy was not restricted by a dependent pup, or prey consumed during the beginning of the breeding season shortly after the occurrence of pupping.

As juvenile male SSL are not under the same constraints as adult female SSL with dependent pups, they may spend more time foraging, travel farther distances from the rookery, and possibly consume prey items similar to adult female NFS. If these two females did not have dependent pups, they may employ a foraging strategy similar to that of the juvenile male. However, since the number of females without pups and juvenile males present on the rookery is very low, the level of inter-specific competition between this particular SSL demographic and NFS is likely to be negligible.

When plotted against PC2 from the combined-years PCA, the two territorial NFS males sampled by remote biopsy were substantially different from the female NFS samples collected in 2008 and located between the female NFS and the direct-biopsied SSL. As with the SSL biopsies, this variance in FA composition is not likely due to sampling location. Although the masses of the remote and direct biopsies were not significantly different ($U = 83$, $p = 0.806$), the diameter of the biopsy tips used for remote and direct samplings of NFS were different (6 mm *vs* 4 mm). Thus, while the remotely biopsied samples were wider, they may have also been shorter as a result of incomplete

penetration of the biopsy tip, possibly due to the dense fur that grows on the neck of male NFS. In this case, the samples may be primarily from the outer blubber layers that represent an earlier diet. However, the variation is more likely due to actual dietary differences between male and female NFS. FA composition and dietary differences have been demonstrated in multiple pinniped species, including gray seals (Beck *et al.* 2005) and New Zealand sea lions (Meynier *et al.* 2008). While guarding their harems, male NFS are less likely to make extended foraging trips long distances from the rookery due to the risk of losing their territory to another male. Instead, they are more likely to make infrequent, short foraging trips within close range of their territory with a subsequent difference in the prey species consumed. The $\delta^{13}C$ and $\delta^{15}N$ levels of a vibrissa collected from a dead male NFS suggest nearshore foraging at a higher trophic level than the female NFS, similar to the SI levels of SSL. Conversely, both the FA and SI profiles of the male NFS samples may represent those of animals not feeding at all, rather than ones with a similar diet to SSL.

The FA composition of the blubber of both species was significantly different between years. This variation may be the result of differences in sampling technique, storage methods, storage time, FA extraction and analysis methods, or temporal differences in prey consumption. Samples collected in 2007 were not flushed with nitrogen gas and were kept at -20°C for several months. Although sealed in airtight containers, these small samples may have experienced more oxidation of FA than samples collected in 2008, resulting in a subsequent loss of information (Budge *et al.* 2006). The use of multiple labs for the analysis of FA samples is not recommended due

to differences in extraction and analysis methods, equipment, and personnel, possibly making the different datasets incomparable to one another. However, despite the significant between-year differences represented by the first PC in the combined-years PCA, the same general pattern of resource partitioning represented by the second PC was exhibited for both years.

CONCLUSIONS

The partitioning of foraging resources by breeding female SSL and NFS indicated by stable nitrogen and carbon isotope analysis of vibrissal roots and fatty acid analysis of blubber is corroborated by data from concurrently-collected scat and spews. Although the exact dietary composition cannot be directly determined using the resultant data, biochemical analyses have several advantages over the analysis of scats and spews and are complementary. Since SI in vibrissal roots and FA in blubber are integrated over a period of weeks to months, they provide dietary information that covers a greater time period than a single scat collection effort. Therefore, events such as short-term influxes of a particular prey species, although often important, are less likely to bias estimates of diet composition over longer time periods. Biochemical analyses can also provide information that is difficult or impossible to obtain when using only undigested prey remains recovered from scats collected on a rookery. Since vibrissae and blubber samples are collected directly from individual animals, comparisons of diet between age-groups, reproductive classes, gender, and species can easily be made. Furthermore, dietary

information can be compared with results from health assessments, including body composition, pregnancy status, disease status, and presence of injuries. To obtain the same information using undigested prey remains, stomach and/or gastrointestinal contents must be collected, which is not always possible. Such data would be subject to many of the same biases associated with scat and spew analysis.

Both FA and SI analyses demonstrated resource partitioning between NFS and SSL. Of the two methods, SI analysis is generally less costly and complicated and the samples are easier and less invasive to obtain. This study did not find a significant difference in stable isotope levels between live and dead animals, further expanding the opportunity to collect samples in a non-invasive manner. Additionally, as stable isotopes are deposited along the length of the vibrissae as they grow, combined with the generally high site-fidelity of SSL and NFS, many years' worth of foraging strategies and dietary resource partitioning patterns can be examined based on the collection effort of a single season. Therefore, unless estimates of proportions of specific prey items are desired and a library of FA profiles of prey, which both spatially and temporally overlaps the study site, is available, the use of stable isotope analysis in conjunction with scat analysis is recommended.

CHAPTER 3. ANALYSIS OF ANIMAL MOVEMENT AND DIVE BEHAVIOR

INTRODUCTION

Partitioning of available resources allows species with similar ecological requirements to coexist within the same geographical region with minimal competition. In the case of pinnipeds, in particular, the resources that are most often limiting include the available prey base and space on land for breeding and rearing their young. Food resources are most commonly partitioned based on prey type, with the sympatrically occurring predator species each targeting different prey species or different sizes of the same prey species (Page *et al.* 2005, Cooper *et al.* 2009). In cases where the species and sizes of the prey items consumed overlap, intra- and inter-specific competition for food resources can be minimized by a spatial partitioning of the foraging grounds (Robson *et al.* 2004, Baylis *et al.* 2008).

The partitioning of forage resources by prey type has been studied in several pinniped species through the identification of undigested prey remains recovered from stomachs, scats, and spews as well as through analysis of stable isotopes and fatty acids (Page *et al.* 2005, Cooper *et al.* 2009, Gross *et al.* 2009, Newland *et al.* 2009, Zeppelin and Orr 2010). Although the concurrent use of more than one of these methods may reduce the biases associated with each individual technique, each has limitations with respect to the time scale represented by the type of sample collected. Furthermore, the existence of a significant dietary overlap as determined through one or more of these

methods may not necessarily be indicative of direct competition between the sympatric predators as the actual foraging location of each predator species cannot always be elucidated from these results alone.

The inter- and intra-specific spatial partitioning of foraging grounds by marine mammals has been studied through the use of satellite-linked time-depth recorders (TDRs) directly attached to the species of interest (Robson *et al.* 2004, Bailleul *et al.* 2005). These instruments are capable of recording dive depth and swim speed, and other environmental and oceanographic variables such as water temperature, light level, and salinity, as well as tracking animal movement and habitat use. With the recent development of GPS tags suitable for use on marine mammals, location and movement can be tracked at high levels of accuracy. Depending on the method used to attach the instruments, pinnipeds can be tracked for up to several months before the batteries fail or the instrument is lost during molt. Thus, it is possible to examine the foraging behavior of a pinniped over the course of its entire breeding season without multiple disturbances of the rookery.

Steller sea lions (SSL, *Eumetopias jubatus*) breed sympatrically with northern fur seals (NFS, *Callorhinus ursinus*) on the Lovushki (48.5436° N, 153.6736° E) Island group in the Kuril Island chain (Figure 2). The abundance of non-pup SSL on Lovushki Island has remained relatively stable from 1995 through 2005 at an average of 1039 SSL (Burkanov and Loughlin 2005). However, a rapid increase in NFS population numbers ensued during the early 21st century and the pup population grew to 12,180 pups by 2006 (Burkanov *et al.* 2007), placing the non-pup population on Lovushki Island at an

estimated 28,420 adult and juvenile NFS. The diets of NFS and SSL at their allopatric sites in the Kuril Islands were similar in the 1950s and 60s (Panina 1964, Belkin 1966, Panina 1966, Kuzin *et al.* 1977) with walleye pollock (*Theragra chalcogramma*) accounting for the majority of the NFS and SSL diet. Thus, based on potentially similar diets and the rapid increase in NFS population numbers, there is substantial potential for inter-specific competition for prey resources on Lovushki Island.

In this study, we examined the spatial partitioning of foraging grounds between sympatrically breeding northern fur seals and Steller sea lions on Lovushki Island, Russia using both satellite-linked and archival TDRs and GPS tags and compare the results with the dietary estimates derived from analysis of scats and spews (Chapter 1), stable isotopes, and fatty acids (Chapter 2).

METHODS

During the breeding seasons of 2007 and 2008 (June through August), 14 adult female northern fur seals and 13 adult female Steller sea lions were captured on Lovushki Island in the Kuril Island chain located in the Russian Far East. In 2007, each animal was instrumented with an Mk10-F TDR with FastLoc GPS receiver (Wildlife Computers, Inc., Redmond, WA), which was attached dorsally to the head using 5-min epoxy. At least one other instrument was attached dorsally, approximately two-thirds towards the tail of each animal, usually a variant of the Mk10 TDR customized to record different variables along with depth measurements. Some NFS were transported back to the support vessel upon

capture prior to instrumentation for other research purposes before being released on or near the rookery. All SSL were instrumented on the rookery. Instruments deployed on NFS and SSL in 2007 were recovered when the animals were recaptured after visual and VHF tracking of the animals indicated that at least one foraging trip had been made. NFS and SSL in 2007 were recaptured between 3–39 and 8–12 d post-deployment, respectively. Instrument deployments for NFS in 2008 were similar; however, SSL were equipped with Mk10-AFL satellite transmitters and did not have to be recaptured to recover the data. Depending on the instrument model, depths were recorded at either 0.5 Hz or 1.0 Hz at a resolution of 0.1 m. Upon examination of the tracking data, it was determined that one SSL had not left the rookery before it had been recaptured and those data were excluded from analysis. Deployment details are summarized in Table 16.

GPS coordinates were calculated from the FastLoc GPS data using software provided by the instrument manufacturer and resultant GPS tracks were analyzed using the R package "trip" (Sumner 2010). Erroneous coordinates were removed based on a maximum swim speed between sequential GPS coordinates of 3 m s^{-1} using an algorithm presented in McConnell *et al.* (1992). Tracks were divided into individual trips based on periods when the animal was hauled out on dry land. Distance and duration of each trip >3 h was measured. Based on movement and dive patterns, trips <3 h were not considered to be representative of foraging effort, but rather representative of departure due to rookery disturbance wherein the animals remained primarily in the surf zone and

Table 16. Summary of instrument deployments for northern fur seals (NFS) and Steller sea lions (SSL) in 2007 and 2008.

Species	ID	Deployment Date	Recovery Date*	Tracking Duration (days)
NFS	NFS-07-03	21-Jun-07	30-Jul-07	38.5
	NFS-07-04	22-Jun-07	30-Jul-07	38.9
	NFS-07-05	22-Jun-07	4-Aug-07	43.2
	NFS-07-24	29-Jul-07	4-Aug-07	5.8
	NFS-07-25	29-Jul-07	4-Aug-07	5.2
	NFS-07-27	31-Jul-07	4-Aug-07	4.4
	NFS-08-01	17-Jul-08	30-Jul-08	12.5
	NFS-08-02	17-Jul-08	29-Jul-08	12.2
	NFS-08-07	18-Jul-08	29-Jul-08	10.7
	NFS-08-09	18-Jul-08	31-Jul-08	12.8
	NFS-08-10	18-Jul-08	29-Jul-08	10.9
	NFS-08-13	20-Jul-08	2-Aug-08	13.3
	NFS-08-14	20-Jul-08	29-Jul-08	8.6
	NFS-08-15	20-Jul-08	30-Jul-08	10.0
SSL	SSL-07-01	9-Jun-07	21-Jun-07	12.1
	SSL-07-04	12-Jun-07	21-Jun-07	8.5
	SSL-07-05	13-Jun-07	21-Jun-07	8.1
	SSL-08-01	20-Jun-08	16-Jul-08	26.7
	SSL-08-02	20-Jun-08	11-Jul-08	21.0
	SSL-08-05	23-Jun-08	5-Aug-08	43.4
	SSL-08-11	21-Jun-08	2-Aug-08	42.0
	SSL-08-12	22-Jun-08	22-Jul-08	30.2
	SSL-08-13	22-Jun-08	4-Aug-08	43.3
	SSL-08-14	22-Jun-08	25-Jul-08	33.1
	SSL-08-15	23-Jun-08	3-Aug-08	41.6
	SSL-08-17	24-Jun-08	4-Aug-08	41.6

*Date of last transmission for satellite-linked instruments

performed few dives. Only complete round-trips that both initiated and terminated on the rookery were analyzed. Trips that began immediately upon release from the support vessel were not included in the analysis.

Depth data collected at 0.5 Hz were sub-sampled to 1 Hz by excluding records recorded on the half-second. No sub-sampling was done in cases where depth data had been collected at 1 Hz. Depths were zero-offset corrected (ZOC) to account for drifts in the calibration of the pressure transducer. Depths were corrected by finding the minimum depth within a 20-minute moving window and then subtracting that depth from all depth measurements within each window.

Dive profiles from TDR records were then analyzed using the R package "diveMove" (Luque 2007). Dives <4 m in depth were excluded from the analysis because they could not reliably be distinguished from the random noise that could not be corrected for during the ZOC procedure. Duration, maximum depth, and post-dive surface interval were determined for each dive, with the dive depth defined as the maximum depth reached within a single dive. A bout ending criterion (BEC) was calculated for each animal by modeling a mixture of two random Poisson processes to the histogram-like data of log frequency versus the interval mid-points of each dive (Sibly *et al.* 1990). Each dive in a series of >5 dives was assigned to a specific bout if its post-dive surface interval was less than the BEC calculated for that particular animal. Dives not meeting these criteria were classified as isolated dives and excluded from further bout analyses. A geographical location was assigned to each bout through a time-based linear interpolation method using the GPS coordinates whose time stamps bounded the

corresponding TDR time stamp for the beginning of the first dive within each bout. A directional vector consisting of the bearing and distance between the bout location and the trip start location, defined as the last on-land GPS coordinate recorded for each trip, was calculated using the R packages "argosfilter" (Freitas 2010) and "sp" (Bivand *et al.* 2008), respectively. Water depth was estimated at each bout location through interpolation of 30-arc-second bathymetric data (The GEBCO_08 Grid, version 20091120, http://www.gebco.net).

Generalized linear mixed models with repeated measures were used to test for differences in dive depth and duration, trip length and duration, and bout location between NFS and SSL and between years. An autoregressive covariance structure of order 1 (AR1) was used to model the serial correlation among observations within each animal. Tukey post-hoc tests were performed on significant interaction terms. For these analyses, V-shaped dives (dives in which the bottom time accounted for <5% of the total dive duration) were excluded as they are considered transit or exploratory dives and not representative of foraging effort (Le Boeuf *et al.* 1988, Kuhn *et al.* 2009). Dives >900 sec were excluded as they were likely the result of instrument error or a failure for the ZOC procedure to correctly separate multiple dives ($n = 6$). Watson's test for circular uniformity was used to examine directionality of bout locations and Watson's two-sample test of homogeneity was used to examine differences in mean bout directions between species.

All means are reported ± SEM. Statistical analyses were performed at the 95% significance level using SAS version 9.1 (SAS Institute Inc, Cary, North Carolina) and R version 2.11.1 (R Development Core Team 2010).

RESULTS

During the period of TDR data collection, 14 NFS performed a total of 25,925 dives. After filtering for erroneously long dives and dives <4 m, 18,241 dives remained for analysis. The mean dive depth and duration for NFS was 18.4 ± 2.2 m and 40.3 ± 8.0 s. The mean maximum dive depth was 75.1 ± 4.2 m. Twelve SSL performed a total of 14,754 dives, of which 14,384 were used for analysis. The mean dive depth and duration for SSL was 43.1 ± 1.4 m and 113.2 ± 13.7 s. The mean maximum dive depth was 240.3 ± 22.1 m (Table 17). The mean dive depth for SSL was significantly deeper than that of NFS ($F_{1,22} = 41.62, p < 0.001$) and the mean dive duration for SSL was significantly longer than that of NFS ($F_{1,22} = 72.11, p < 0.001$). The mean maximum dive depth for SSL was significantly deeper than that of NFS (Welch's $t_{11.9} = 7.39, p < 0.001$). SSL made the majority of their dive bouts in waters <150 m (cumulative percentages: 68.2% <50m, 85.3% <100m, 90.3% <150m). NFS made only 16.9% of their dive bouts in waters <150m, while 76.7% of bouts were made in waters >500 m depth.

A total of 74 forging trips were made by NFS during the period of GPS data collection (Table 18, Figure 11). The mean trip length and duration made by NFS was 112.6 ± 13.9 km and 44.6 ± 5.6 h. SSL made 236 foraging trips (Figure 12) with a mean

Table 17. Summary of dive depth and duration for northern fur seals (NFS) and Steller sea lions (SSL) in 2007 and 2008.

Species	ID	Total dives	Max depth (m)	Mean depth ± SEM (m)	Max duration (sec)	Mean duration ± SEM (sec)
NFS	NFS-07-03	2421	84.0	12.1 ± 0.2	190	29.8 ± 0.5
	NFS-07-04	1557	70.5	9.5 ± 0.2	204	26.4 ± 0.7
	NFS-07-05	2879	64.0	12.4 ± 0.2	200	32.8 ± 0.5
	NFS-07-24	422	57.0	24.4 ± 0.5	134	56.8 ± 1.1
	NFS-07-25	857	82.5	25.4 ± 0.5	105	45.6 ± 0.7
	NFS-07-27	526	59.0	24.6 ± 0.5	109	53.2 ± 1.0
	NFS-08-01	774	59.5	19.6 ± 0.4	133	46.9 ± 1.1
	NFS-08-02	1625	89.5	21.5 ± 0.4	403	41.3 ± 0.8
	NFS-08-07	1132	93.5	22.2 ± 0.5	207	44.5 ± 1.0
	NFS-08-09	1927	102.5	15.8 ± 0.2	226	44.4 ± 0.7
	NFS-08-10	765	90.0	19.3 ± 0.6	150	36.0 ± 1.0
	NFS-08-13	1761	66.0	20.3 ± 0.2	172	32.8 ± 0.5
	NFS-08-14	950	45.0	11.1 ± 0.2	329	34.3 ± 1.0
	NFS-08-15	645	69.0	20.0 ± 0.6	150	39.8 ± 1.2
	Summary	**18,241**	**102.5**	**18.1 ± 2.2**	**403**	**40.3 ± 8.0**
SSL	SSL-07-01	396	278.0	32.5 ± 2.4	197	59.7 ± 3.3
	SSL-07-04	101	146.0	68.8 ± 5.2	372	150.8 ± 9.6
	SSL-07-05	70	115.5	49.9 ± 4.2	337	163.4 ± 12.5
	SSL-08-01	1181	196.0	36.1 ± 1.2	344	101.8 ± 2.3
	SSL-08-02	452	180.0	42.0 ± 2.2	360	112.5 ± 4.0
	SSL-08-05	2753	328.0	34.3 ± 0.9	1280	97.9 ± 1.6
	SSL-08-11	603	152.0	30.1 ± 1.5	352	110.1 ± 3.6
	SSL-08-12	1720	280.0	36.0 ± 0.9	400	103.8 ± 1.8
	SSL-08-13	1751	304.0	39.7 ± 1.0	480	96.4 ± 1.7
	SSL-08-14	2562	288.0	19.3 ± 0.7	444	71.6 ± 1.4
	SSL-08-15	1547	296.0	42.5 ± 1.3	344	105.9 ± 2.1
	SSL-08-17	1248	320.0	47.4 ± 1.5	368	131.1 ± 2.4
	Summary	**14,374**	**328.0**	**43.1 ± 1.4**	**1280**	**113.2 ± 13.7**

Table 18. Summary of foraging trip durations and distances for northern fur seals (NFS) and Steller sea lions (SSL) in 2007 and 2008.

Species	ID	Trips	Max Trip Duration (h)	Mean Trip Duration ± SEM (h)	Max Trip Distance (km)	Mean Trip Distance ± SEM (km)
NFS	NFS-07-03	14	124.2	34.9 ± 11.6	282.7	89.0 ± 29.6
	NFS-07-04	15	128.5	29.5 ± 12	366.2	74.2 ± 33.5
	NFS-07-05	18	163.6	36.2 ± 11.0	223.9	87.3 ± 24.0
	NFS-07-24	1	121.6	121.6 ± 0.0	360.5	360.5 ± 0.0
	NFS-07-25	1	118.5	118.5 ± 0.0	341.0	341.0 ± 0.0
	NFS-07-27	1	92.7	92.7 ± 0.0	165.4	254.2 ± 0.0
	NFS-08-01	1	133.1	133.1 ± 0.0	293.7	293.7 ± 0.0
	NFS-08-02	2	103.7	94.7 ± 9.1	239.3	217.1 ± 22.2
	NFS-08-07	3	82.1	59.6 ± 22.2	245.8	172.0 ± 62.1
	NFS-08-09	3	103.4	78.8 ± 18.7	283.5	201.2 ± 58.3
	NFS-08-10	6	86.8	25.2 ± 12.4	310.9	96.6 ± 43.3
	NFS-08-13	3	137.5	77.7 ± 39.2	267.2	154.2 ± 78.2
	NFS-08-14	2	131.8	80.1 ± 51.8	269.0	165.4 ± 103.5
	NFS-08-15	4	88.7	26.3 ± 20.9	171.9	55.3 ± 40.4
	Summary	**74**	**163.6**	**44.6 ± 5.6**	**366.2**	**112.6 ± 13.9**
SSL	SSL-07-01	4	10.0	7.3 ± 1.4	35.4	21.7 ± 7.3
	SSL-07-04	2	7.5	7.5 ± 0.0	18.1	17.8 ± 0.3
	SSL-07-05	–*	–*	–*	–*	–*
	SSL-08-01	21	31.9	13.9 ± 1.9	34.5	14.4 ± 1.8
	SSL-08-02	16	58.1	13.9 ± 3.2	36.3	12.5 ± 2.5
	SSL-08-05	37	53.2	13.4 ± 2.0	82.8	17.9 ± 2.9
	SSL-08-11	17	69.2	23.2 ± 5.4	57.1	17.1 ± 3.3
	SSL-08-12	32	42.6	9.9 ± 1.4	26.7	9.3 ± 1.2
	SSL-08-13	23	70.9	18.7 ± 3.6	77.7	21.8 ± 4.0
	SSL-08-14	26	78.3	18.0 ± 3.3	66.5	20.6 ± 3.4
	SSL-08-15	28	72.0	21.4 ± 3.9	166.8	34.8 ± 7.4
	SSL-08-17	30	66.9	16.4 ± 2.4	37.5	17.4 ± 1.9
	Summary	**236**	**78.3**	**14.3 ± 3.9**	**166.8**	**26.7 ± 1.2**

*Not analyzed due to problems with the GPS data

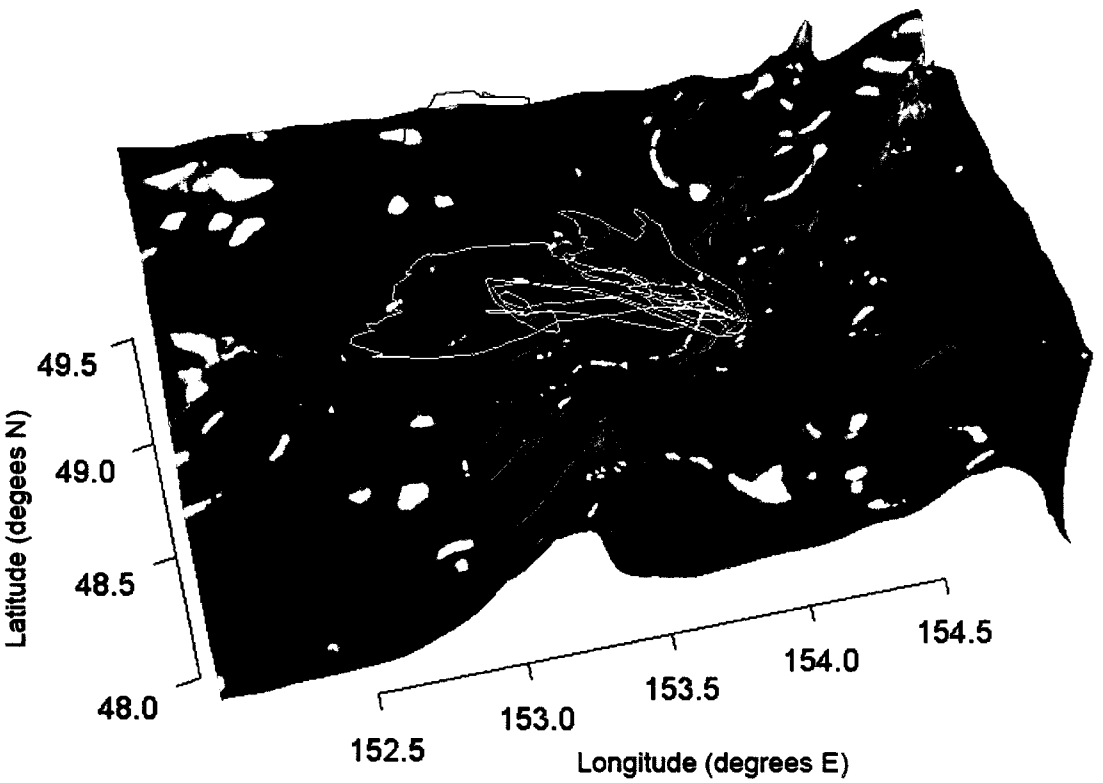

Figure 11. Plot of typical foraging trips made by two northern fur seals in 2007 (red) and 2008 (yellow).

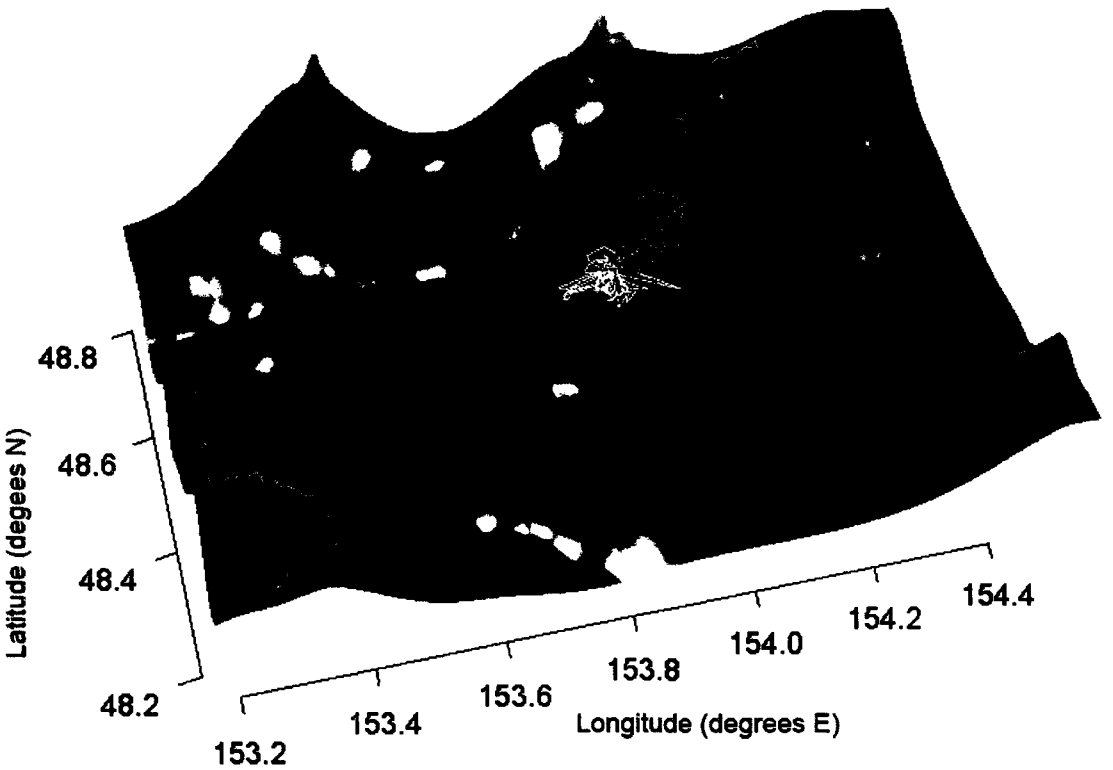

Figure 12. Plot of typical foraging trips made by two Steller sea lions in 2007 (red) and 2008 (yellow).

trip length and duration of 26.7 ± 1.2 km and 14.3 ± 3.9 h. Trips made by NFS were significantly longer in both distance ($F_{1,22} = 59.56, p < 0.001$) and duration ($F_{1,22} = 42.69, p < 0.001$) than those made by SSL.

NFS made a total of 669 diving bouts with a mean distance and bearing from land of 41.9 ± 3.5 km and 303.4 ± 2.8 degrees (Table 19, Figure 13). SSL made 488 bouts with a mean distance and bearing from land of 3.1 ± 2.2 km and 131.1 ± 3.3 degrees (Figure 14). Bouts made by NFS were significantly further from land ($F_{1,21} = 46.52, p < 0.001$) and in a significantly different direction (Watson's test of homogeneity, $U = 0.3719, p < 0.01$) than those made by SSL. Both SSL (Watson's test of uniformity, $U^2 = 4.48, p < 0.01$) and NFS ($U^2 = 18.50, p < 0.01$) bout locations exhibited strong directionality (Figure 15). Bouts made by NFS in 2007 (298.0 ± 82.0 degrees) were in a significantly different direction from those made in 2008 (252.8 ± 55.1 degrees) ($U = 2.20, p < 0.001$).

DISCUSSION

Adult female SSL and NFS on Lovushki Island foraged in significantly different locations, thus spatially partitioning the foraging grounds and reducing the amount of inter-specific competition for prey resources. Female SSL focused most of their foraging effort in the shallow waters within 3.1 km of the rookery (Figure 12). Almost 70% of dive bouts occurred in waters <50 m depth (Figure 14) and the average dive depth of 43.1 m suggests that SSL primarily foraged benthically, as illustrated by plots of TDR data.

Table 19. Summary of dive bouts and bout ending criteria (BEC) for northern fur seals (NFS) and Steller sea lions (SSL) in 2007 and 2008.

Species	ID	BEC (s)	Total bouts	% of dives occurring in bouts	Mean dives per bout ± SE	Mean bout duration ± SE (mins)	Mean bout distance ± SE (km)	Mean bout bearing ± SE (deg)
NFS	NFS-07-03	65.6	101	70.1	27.4 ± 3.4	17.5 ± 1.7	47.3 ± 2.5	309.9 ± 3.9
	NFS-07-04	101.1	88	73.9	24.7 ± 3.0	16.6 ± 1.8	85.0 ± 4.7	333.6 ± 5.9
	NFS-07-05	71.7	148	64.3	21.9 ± 2.2	16.8 ± 1.4	41.8 ± 2.0	308.3 ± 3.0
	NFS-07-24	97.9	15	77.1	25.4 ± 5.1	40 ± 10.3	42.8 ± 1.3	277.7 ± 4.0
	NFS-07-25	50.3	19	75.7	36.4 ± 10.3	39.3 ± 9	55.1 ± 4.8	281.8 ± 3.1
	NFS-07-27	53.4	16	78.8	28.0 ± 9.8	39.9 ± 10	58.8 ± 2.2	297.4 ± 7.2
	NFS-08-01	67.2	27	75.4	25.0 ± 4.6	26.7 ± 5.1	62.8 ± 4.2	277.9 ± 2.1
	NFS-08-02	53.5	31	78.8	47.5 ± 9.9	41.8 ± 7.5	50.3 ± 3.6	274.5 ± 1.2
	NFS-08-07	42.3	35	64.1	28.5 ± 6.2	16.1 ± 2.7	34.9 ± 3.2	303.1 ± 5.9
	NFS-08-09	50.9	58	62.2	25.2 ± 4.2	23.4 ± 3.1	24.3 ± 1.6	133.3 ± 6.0
	NFS-08-10	64.0	25	53.4	21.4 ± 5.4	19.7 ± 3.9	23.7 ± 3.0	314.8 ± 12.5
	NFS-08-13	44.4	50	70.7	27.6 ± 4.3	22.5 ± 3.2	31.6 ± 3.0	326.6 ± 9.1
	NFS-08-14	58.02	38	75.7	32.7 ± 15.5	17.2 ± 2.8	46.0 ± 3.4	252.0 ± 3.6
	NFS-08-15	68.93	18	76.8	33.1 ± 15.1	31.4 ± 7.4	17.8 ± 3.0	175.1 ± 8.2
	Summary		**669**	**69.6**	**27.8 ± 0.2**	**21.5 ± 0.8**	**41.9 ± 3.5**	**303.4 ± 2.8**
SSL	SSL-07-01	143.6	21	68.8	18.9 ± 4.9	24.7 ± 5.5	4.0 ± 0.9	102.7 ± 5.2
	SSL-07-04	264.1	7	70.1	13.7 ± 4.4	40.7 ± 15.4	1.8 ± 0.5	79.4 ± 7.3
	SSL-07-05	211.7	7	72.8	21.7 ± 8.2	30.6 ± 11.6	–*	–*
	SSL-08-01	179.2	33	83.5	29.9 ± 5.6	813.3 ± 141.6	2.7 ± 0.34	229.0 ± 7.2
	SSL-08-02	140.2	21	61.7	13.3 ± 1.9	219 ± 47.8	2.9 ± 0.5	177.2 ± 15.9
	SSL-08-05	111.9	86	71.8	23.0 ± 2.8	206.4 ± 22.3	3.8 ± 0.5	115.5 ± 4.3
	SSL-08-11	243.7	22	85.2	23.4 ± 3.0	919.3 ± 196	17.8 ± 4.6	95.9 ± 3.6
	SSL-08-12	148.8	50	90.1	31.2 ± 3.3	367.8 ± 52.0	2.3 ± 0.3	122.9 ± 5.9
	SSL-08-13	158.5	73	58.6	14.1 ± 1.3	216.4 ± 25.3	6.9 ± 0.9	92.6 ± 4.0
	SSL-08-14	114.3	47	87.2	46.6 ± 13.9	337.2 ± 48.7	4.1 ± 0.6	119.4 ± 6.5
	SSL-08-15	182.9	65	72.3	17.2 ± 1.2	317.5 ± 39.4	4.3 ± 0.5	137.8 ± 4.8
	SSL-08-17	148.1	56	62.7	14.0 ± 1.3	217.3 ± 29	2.8 ± 0.2	140.8 ± 6.4
	Summary		**488**	**75.2**	**20.1 ± 1.1**	**29.1 ± 1.3**	**3.1 ± 2.2**	**131.1 ± 3.3**

*Not analyzed due to problems with GPS data

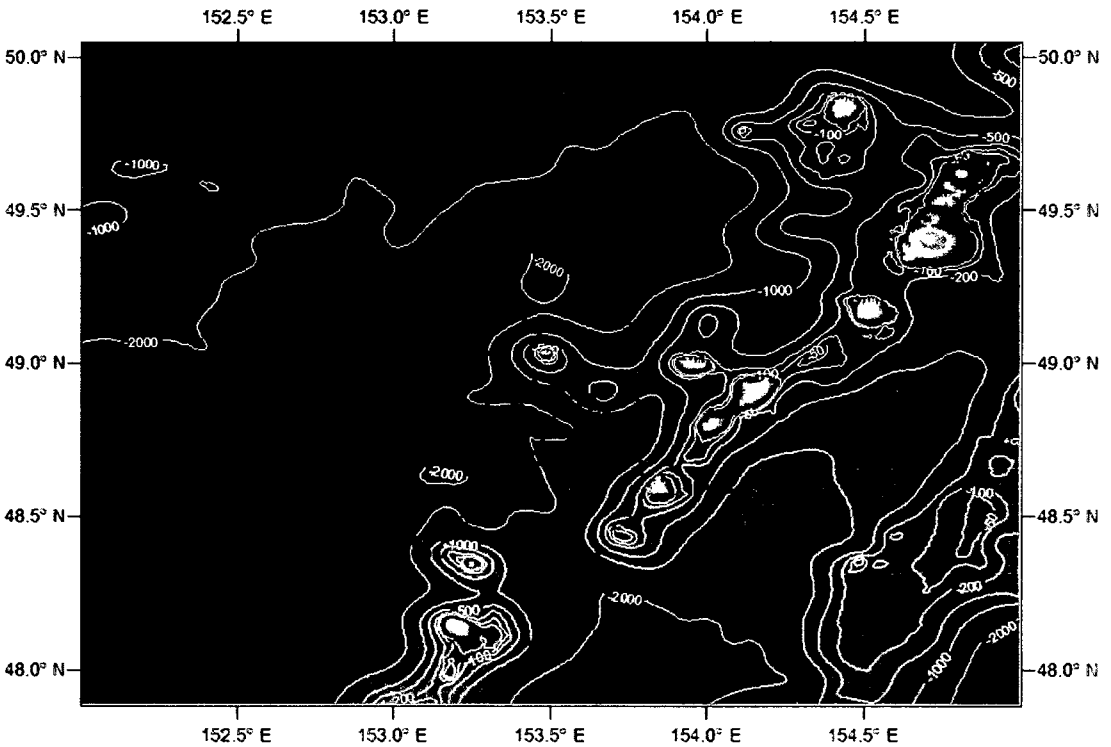

Figure 13. Locations of northern fur seal foraging bouts combined for 2007 and 2008 (red dots). Yellow triangle marks the location of Lovushki Island.

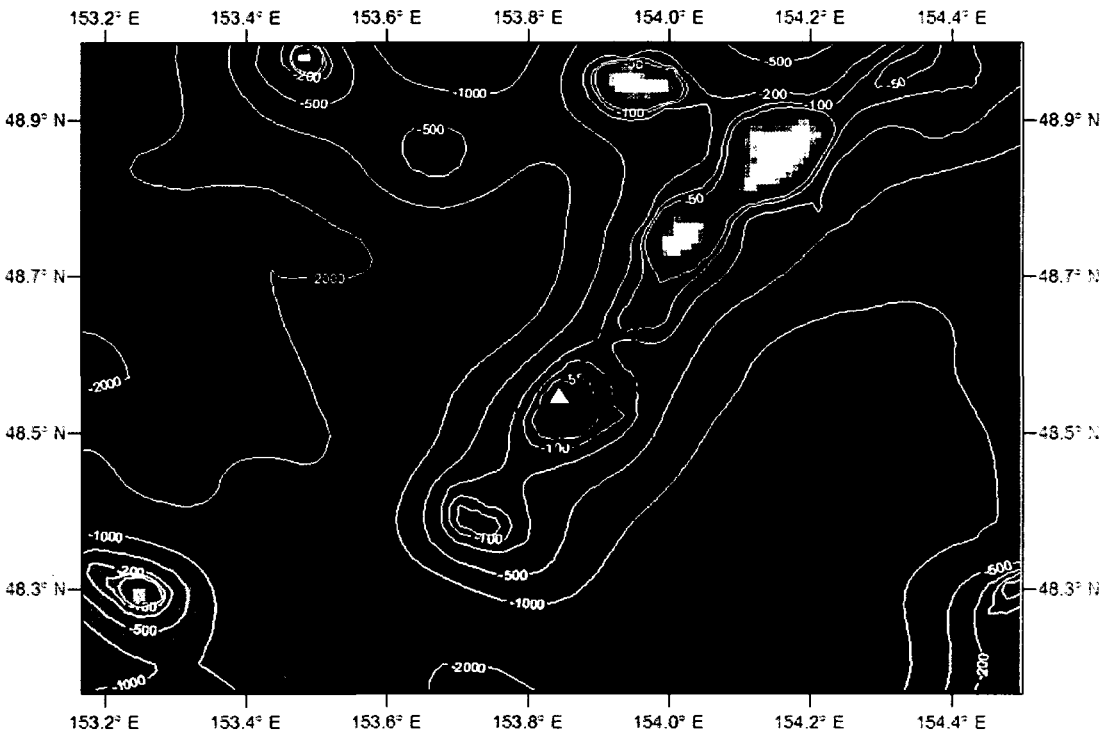

Figure 14. Locations of Steller sea lion foraging bouts combined for 2007 and 2008 (red dots). Yellow triangle marks the location of Lovushki Island.

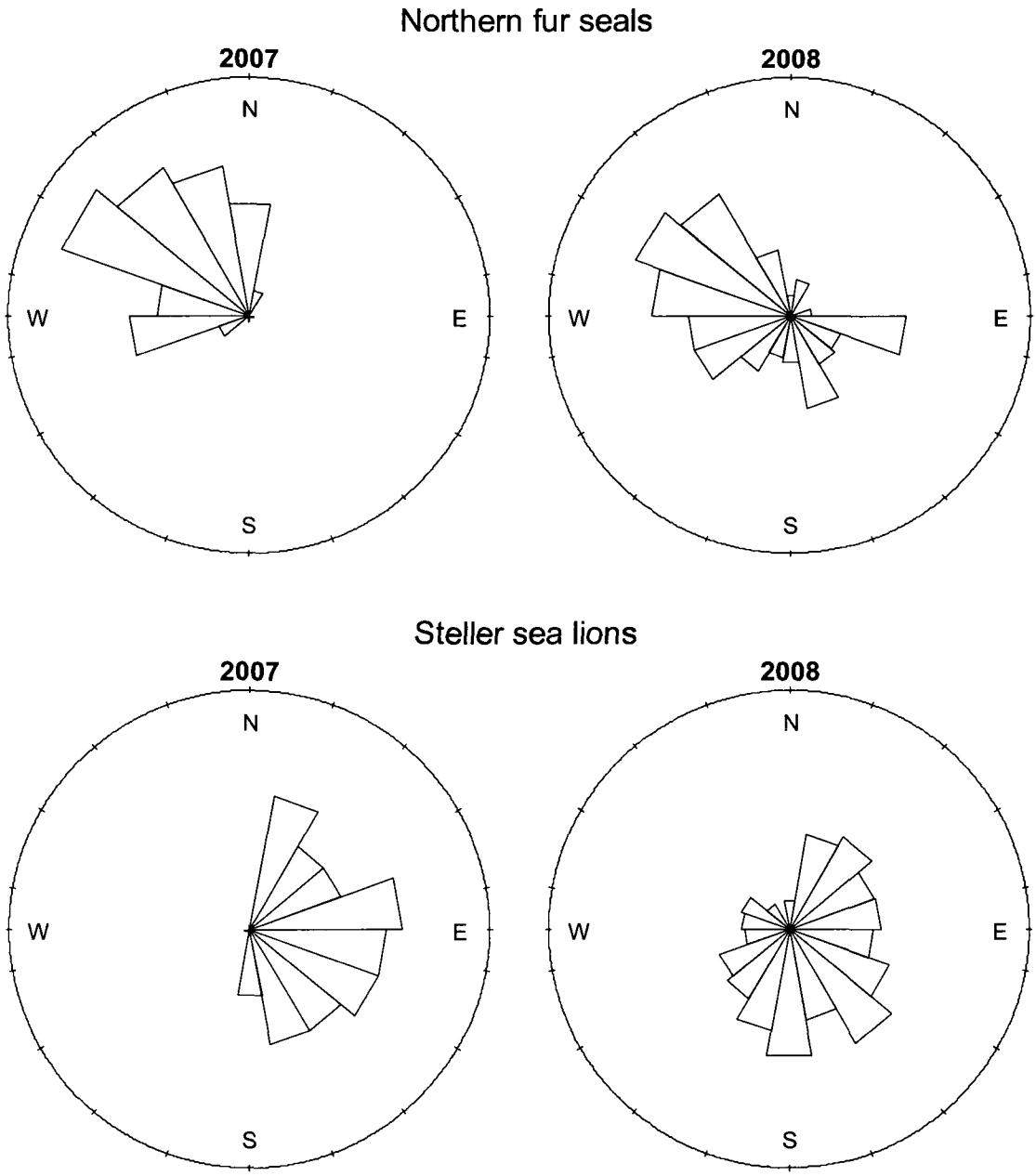

Figure 15. Rose diagrams of northern fur seal (top) and Steller sea lion (bottom) bout location bearings from Lovushki Island in 2007 and 2008. Area of each sector is proportional to the frequency.

The top panels of Figure 16 show a series of flat-bottomed dives of increasing depth, indicative of benthic foraging (Hindell *et al.* 1991, Le Boeuf *et al.* 1992, Gales and Mattlin 1997, Merrick and Loughlin 1997, Thompson *et al.* 1998) as the sea lion moved farther away from the rookery into deeper water. In contrast, NFS females traveled much greater distances than SSL, foraging an average of 41.9 km from the rookery (Figure 11) in the waters of the northern Kuril Basin in the Sea of Okhotsk. While the average dive depth of NFS was 18.1 m, the majority of dive bouts took place in water depths of >500 m (Figure 13), indicating that the NFS foraged pelagically rather than benthically. The lower panels of Figure 16 show a series of shallow dives that exhibit a substantial amount of wiggle during the bottom phase of the dive, indicative of pelagic foraging (Gentry *et al.* 1986b, Bengtson and Stewart 1992, Schreer and Testa 1996).

NFS foraged primarily at night and focused their foraging effort within a narrow window of time centered on midnight; 92.8% (n = 621) of dive bouts occurred between the hours of 20:00 and 04:00. This behavior is consistent with that of other fur seal species feeding on pelagic vertically migrating prey items (Trillmich *et al.* 1986, Goebel *et al.* 1991, Bengtson and Stewart 1997, Georges *et al.* 2000). SSL also foraged primarily at night, but substantial foraging effort began much earlier in the afternoon; 17.2% (n = 83) of dive bouts occurred between the hours of 14:00 and 20:00, and 71.7% (n = 345) of dive bouts occurred between the hours of 20:00 and 04:00. Additionally, NFS foraged much less during the day (06:00 to 18:00) than SSL (4.8% and 17.2% of dive bouts, respectively), presumably because their prey has migrated to deeper, inaccessible depths during the day.

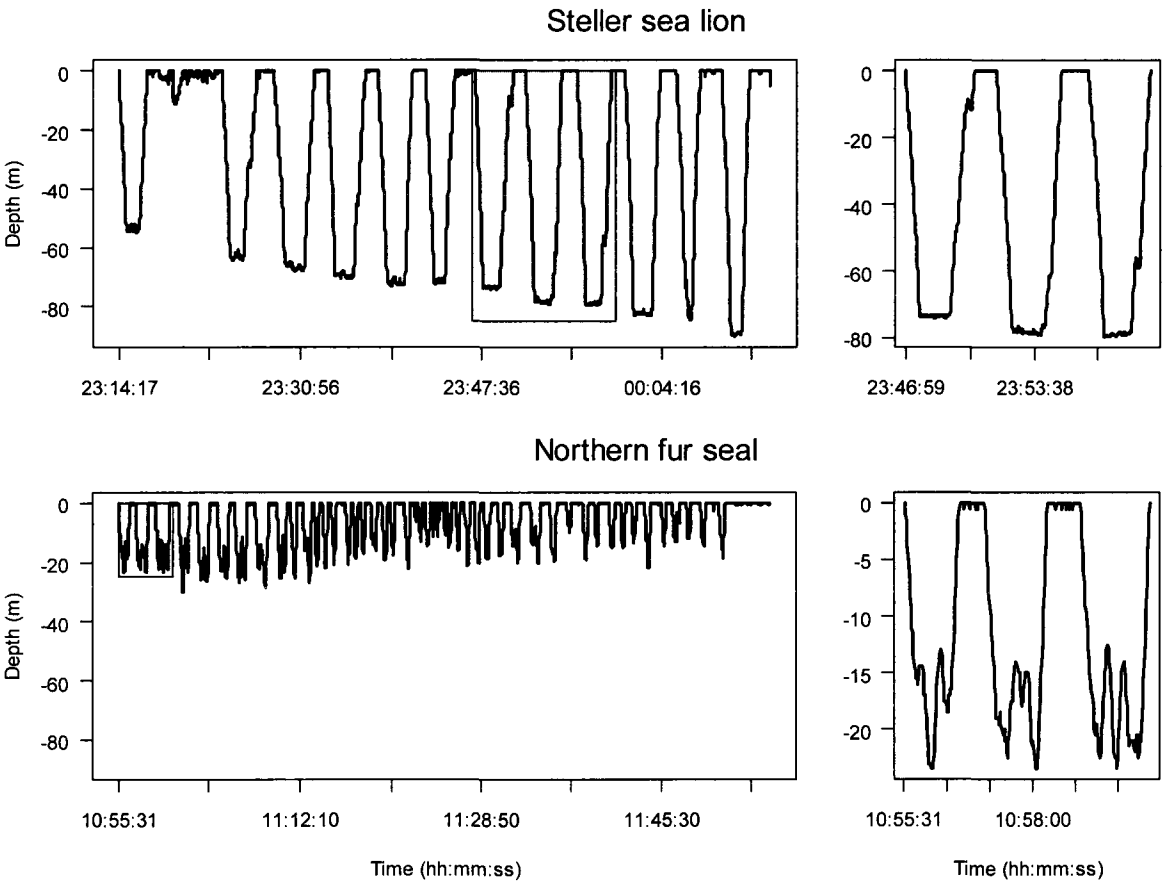

Figure 16. Time-depth trace of typical Steller sea lion (upper panel) and northern fur seal (lower panel) dives on Lovushki Island in 2007 and 2008. Left panels represent 1 hour. Right panels represent the 3 individual dives highlighted by the grey boxes.

The expected prey types encountered through these types of foraging behavior fit our expectations based upon estimates of diet composition and foraging locations presented in Chapters 1 and 2. Analysis of scats collected on Lovushki Island in 2007 and 2008 indicated that female SSL feed almost exclusively on Atka mackerel (*Pleurogrammus monopterygius*) (Chapter 1). During the summer, Atka mackerel migrate to shallow waters to spawn, living benthically at depths from the inter-tidal zone to <200 m (Gorbunova 1962, McDermott and Lowe 1997). Lovushki is situated on a narrow, shallow shelf that extends approximately 40 km southwest from the southern tip of Shiashkotan Island (48.7° N 154.0° E). Sea floor depths >200 m occur within 7–8 km of Lovushki, resulting in a relatively small region with suitable bathymetry for spawning Atka mackerel, thus concentrating this prey species within a very short distance from the rookery. The sea floor depth increases at a higher rate northwest of the rookery where depths >200 m occur in as little as 3 km. Therefore, SSL made far fewer foraging bouts in this direction and concentrated their foraging effort in directions where water depths increased less rapidly. In addition to diving deeper than NFS, SSL also dove for longer durations. Atka mackerel are a relatively cryptic species, often hiding amongst the rocks and kelp during the spawning season (Gorbunova 1962), which may increase the amount of time required to be located and captured by predators (Bowen *et al.* 2002). In addition to the increased time necessary to transit to the deeper depths and then return to the surface, the longer dive duration may also be in part due to an increased search time. This is also illustrated by the substantially longer bottom times of dives made by SSL compared to the typical dives made by NFS.

Analysis of NFS scats and spews collected on Lovushki in 2007 and 2008 indicated that female NFS fed primarily on squid (*Gonatopsis* sp.) and northern smoothtongue (*Leuroglossus schmidti)*. Gonatid squid are characterized by distinct diurnal migrations to the epipelagic zone at night (Nesis 1989). Trawl studies conducted in the Sea of Okhotsk by Lapko (1996) in 1989–1993 found that *G. borealis* made up approximately 97% (43.0–77.3 thousand tons) of the squid biomass that migrated to the epipelagic zone at night. Watanabe *et al.* (2006) examined the vertical migration patterns of squid off northern Japan and found that *G. borealis* is found at depths of 500–700 m during the day where the temperatures are typically 3–5° C and migrate to the epipelagic layers at night, where the water temperature rapidly increases to 5–10° C beginning at 100 m. A similar temperature profile, albeit slightly colder, can be found in the waters off Lovushki where the NFS in the present study concentrated their foraging efforts. During the summer months, an influx of warm water from the Sea of Japan through the Soya Straight causes two anticyclonic eddies to form in the southern Sea of Okhotsk (Wakatsuchi and Martin 1991). The upper 100 m of these eddies are characterized by water that is warmer and more saline, while the lower layers are characterized by water that is colder and less saline, compared to the surrounding waters of the Kuril Basin. In July, water temperatures in the upper 100 m reach almost 8° C and quickly drop to 1–2° C below 100 m. The strongest of these eddies has a diameter of 100–200 km and usually forms approximately 240 km to the west of Lovushki Island. Thus, with a mean foraging bout distance of 41.9 km, it is likely that the NFS in this study foraged at the edge of this eddy to exploit abundant aggregations of squid. Northern smoothtongue are located at

depths of 200–1000 meters during the day but migrate to 0–200 m at night (Sobolevskii and Sokolovskaya 1994, Sobolevskii *et al.* 1996). Furthermore, northern smoothtongue have the highest biomass of any mesopelagic fish in the Sea of Okhotsk (Il'inskii and Gorbatenko 1994) and annually consume 2 million tons of larval and small squid (Lapko 1996). Thus, a strong correlation between the distribution of squid and northern smoothtongue would be expected, and NFS foraging on squid would also likely take advantage of the presence of an abundant prey item with a higher energy density. This is reflected in the strong correlation in the occurrence of these two prey items in NFS scats and spews collected on Lovushki (Chapter 1).

The foraging behavior exhibited by SSL and NFS also support our estimates of diet composition and foraging location estimated by biochemical analyses of vibrissal roots and blubber (Chapter 2). Relatively high mean levels of $\delta^{13}C$ stable carbon isotopes measured in vibrissal roots of female SSL indicated that SSL foraged nearshore and benthically, while relatively low mean levels of $\delta^{13}C$ indicated that NFS foraged primarily offshore and pelagically. Though there was not a difference in the distance between bout locations and the rookery or in average dive depth between 2007 and 2008, there was a significant difference in direction traveled during between years. In 2007, NFS foraged primarily northwest of the rookery and in 2008 foraged mainly due west of the rookery. These shifts in foraging location may be due, in part, to the distribution of many pelagic prey items, such as Gonatid squid and northern smoothtongue, which is largely dependent on non-stationary oceanographic features, such as warm- or cold-water eddies and localized elevated chlorophyll concentrations. For example, there was a 20 km

shift in the main anticyclonic eddy that forms each summer in the Kuril Basin between 1977 and 1978 (Wakatsuchi and Martin 1991). However, there was a significant increase in stable nitrogen isotope levels in the vibrissal roots of breeding NFS from 2007 to 2008 (Chapter 2) and scat and spew data indicated a substantial increase in the consumption of cephalopods and a concurrent decrease in the consumption of northern smoothtongue (Chapter 1). As both of these prey types are pelagic, migrate vertically to shallower depths at night and return to deeper waters during the day, and generally aggregate in dense schools during the breeding season, it would be difficult to elucidate this dietary shift based on TDR data alone. While less conclusive, differences in certain fatty acids found in the blubber of NFS and SSL in 2007 and 2008 suggest Atka mackerel and northern smoothtongue as potential prey items for SSL and NFS, respectively.

Choice in foraging location by SSL and NFS may be influenced by the fasting ability of their pups as differences in foraging location affect the length of time a dependent pup must fast while the female is at sea foraging. SSL pups show a rapid metabolic adaptation to fasting with an increased reliance on lipid catabolism within 16 hours of the onset of a fast but begin to lose lean body tissue after reverting to protein catabolism after approximately 2.5 days of fasting (Rea *et al.* 2000). Adult female SSL would be unable to travel the 40 km to the edge of the seasonal Kuril Basin eddy to take advantage of the abundant, high-energy northern smoothtongue before their pups began to lose significant body mass. The mean SSL foraging trip duration of SSL of approximately half a day and mean distance between the rookery and foraging locations of only 3.1 km likely reflects a balance between acquiring larger amounts of an abundant,

but lower energy density prey item such as Atka mackerel, reducing the cost of transport associated with extended foraging trips, and reducing their trip durations to within the fasting limits of their young. While the fasting capability of NFS pups has not yet been studied, Antarctic fur seal (*Arctocephalus gazella*) pups begin to spare protein within 2–3 days after the onset of a fast and do not revert to protein catabolism until at least after day 5 (Arnould *et al.* 2001). Optimal patch choice is partly decided by the extent of competition for prey within a given area (Pyke *et al.* 1977) and in response to reduced prey availability, such as might occur when competition for prey resources is high, predators can choose to modify their prey choice and foraging location. Therefore, the adult female NFS in this study may have increased their trip duration and distance to exploit richer prey sources in order to reduce inter-specific competition with the larger SSL while staying within the fasting abilities of their dependent pups.

CONCLUSIONS

The adult female SSL and NFS on Lovushki Island forage in significantly different locations with very little overlap. The clear spatial partitioning of the foraging grounds, based on only the directionality and distance from shore of dive bout locations, allows both to coexist within the same geographical region despite an increase in the population of both predator species. This partitioning of geographic space likely reflects the differences in foraging abilities of the adults, the fasting abilities of their pups, and the local bathymetric and oceanographic conditions. However, no information is

currently available regarding the foraging location of non-breeding NFS. There is a significant overlap between the diets of breeding SSL and non-breeding NFS (Chapter 1), and as non-breeding NFS outnumber the SSL by an order of magnitude, there is substantial potential for inter-specific competition for dietary resources between these two groups, especially if there is a significant overlap in foraging range. Further, the occurrence of an ecological perturbation impacting the existing prey resources for either species could also substantially increase the potential for inter-specific competition.

GENERAL CONCLUSIONS

This study found significant differences in the dietary composition and foraging location among sympatrically breeding Steller sea lions and northern fur seals on Lovushki Island, Russia. This clear partitioning of resources allows the breeding members of these two ecologically similar species to co-exist within the same geographical region by minimizing the potential for inter-specific competition. However, there is a biologically important overlap in the diets of breeding SSL and juvenile NFS and a continued increase in the juvenile NFS population could result in the competitive exclusion of SSL due to an increased level of competition between these two groups for a limited resource.

Methodologies

The analysis of undigested prey remains recovered from scats and spews provided the highest resolution data on diet composition. Individual prey items were identified down to species in most cases, and the relative sizes and minimum number of individuals consumed could be estimated, which allowed a detailed comparison of diet composition among breeding female SSL, breeding female NFS, and juvenile NFS. A common criticism of the use of scat analysis is that the metrics of percent frequency of occurrence and percent numerical abundance, as defined in Chapter 1, are relatively coarse and not

very informative. The technique of biomass reconstruction, wherein the total mass of ingested prey is estimated based on the sizes of undigested prey remains recovered from scats and spews, is sometimes recommended in order to more accurately assess dietary composition. While biomass reconstruction, in theory, may provide better estimates of energetic intake, this technique introduces additional biases while considerably compounding existing ones. Biomass reconstruction relies first on an accurate measurement of the minimum number of individual prey items consumed, which is greatly influenced by factors such as differential digestion of smaller prey items, regurgitation of larger prey remains, voiding of gastrointestinal contents while at sea, and deposition of elements from a single meal across multiple scats. Secondly, there must be an accurate means by which to estimate the mass of a prey item from any given element recovered from a scat. This is often accomplished through the use of an intermediate predictive equation relating element size to prey length before a predictive equation relating prey length to prey mass is applied. An integral part estimating prey mass from the size of an individual skeletal element is the accurate reconstruction of the original size of the prey element. Different elements from different prey items will have undergone varying degrees of erosion, often making size reconstruction difficult or impossible (Tollit *et al.* 2004). Each of these steps introduces its own set of compounding biases and uncertainty. Many prey items are identified through the use of elements whose size is not easily related to prey mass due to the wide range of sizes of these particular elements within a single individual. Examples of such elements include gill rakers, vertebrae, ribs, teeth, and scales. It is also not possible to estimate the number of individual prey items

consumed based on these elements, and thus the biomass estimate would be just as biased as percent numerical abundance. Additionally, some prey elements only allow the identification of a prey item to family or genus, the members of which may vary widely in size by species (e.g., salmon), making an accurate estimation of biomass impossible. Although substantial effort is underway to address most of these problems by means of captive feeding studies, there is still no accurate means by which to estimate the biomass of prey consumed by an individual free-ranging SSL or NFS. Though subject to their own biases, the metrics of percent frequency of occurrence and percent numerical abundance provide good estimates of foraging effort of the rookery population as a whole, rather than the energetic intake of individuals. This type of estimate, with respect to the prey species targeted and the relative number of prey items consumed, may be more pertinent to the question of resource partitioning than estimates of energetic intake.

The results of biochemical analyses of both vibrissae and blubber showed obvious dietary differences between breeding NFS and SSL. Isotopic analysis of vibrissal roots demonstrated a difference in both the trophic levels on which NFS and SSL on Lovushki Island fed, as well as in their relative foraging locations. While exact prey species cannot be determined, many years' worth of data on foraging trends, at up to a 2-week resolution, could be inferred based on the analysis of sequential sections of a single vibrissa, as well as the foraging patterns of that animal's mother while it was a pup *in utero*. On a shorter time scale, the longitudinal analysis of samples collected towards the end of the breeding season may reveal temporal patterns relating to the perinatal period and weaning, as well as potential changes in foraging behavior due to arrival of conspecifics over the course of

that breeding season. The significant difference in the fatty acid composition of NFS and SSL blubber implied a significant difference in their diets. However, specific prey species could not be determined based on the available data and the extent to which any of the differences were due to FAs that were biosynthesized by the animal as opposed to those that were ingested could not be ascertained. The data from this technique could be used in a quantitative analysis, in which proportions of specific prey items in the diet are estimated, if a library of FA profiles of the prey items occurring in this region were available.

The analysis of animal movement through satellite telemetry corroborated the results of all three of the previous methods in terms of foraging location and inferred prey types consumed and provided high-resolution data on the foraging behavior of breeding NFS and SSL. Even without information on the dietary composition of either predator species, the clear-cut spatial partitioning of the foraging grounds is enough evidence to suggest a reduced level of inter-specific competition for prey among breeding NFS and SSL. The question of competition between juvenile NFS and breeding SSL may be answered through the simultaneous deployment of time-depth recorders and GPS instruments on individuals from both groups.

This is the first study to simultaneously apply the analysis of scats, stable isotopes, fatty acids, and animal movement to examine the use of foraging resources by sympatrically breeding marine mammals. The clear difference in diet composition and foraging location among adult female NFS and SSL was corroborated on multiple time scales by all four methodologies. Each methodology unequivocally pointed to a distinct

partitioning of resources by breeding NFS and SSL on Lovushki Island, and in this case, any one of the analytical techniques could have been selected as the only method used and the same general conclusion would have been reached. However, each technique provided different and complementary pieces of information that allowed the development of a more complete description of the partitioning dynamics. It is possible that data from the application of one of these methods at a different study location may suggest an absence of resource partitioning based on a single dimension of partitioning, such as prey species and size selection. The validity of this conclusion could only be confirmed by examining other dimensions, such as spatial or temporal partitioning, using one of the other techniques. Thus, it is recommended that multiple analytical methods be employed when examining the use of resources by sympatrically occurring animals.

Resource partitioning patterns

A simple explanation for the patterns of resource partitioning exhibited by NFS and SSL on Lovushki Island is the need to reduce inter-specific competition. However, this over-simplified explanation does not provide a mechanism with which to explain why the resources on Lovushki Island are partitioned the way they are, and does not exclude the possibility of arbitrarily or randomly selected foraging behaviors by one species, with the other species doing the opposite simply to reduce competition. It is unlikely that the differences in prey species and foraging location selection are arbitrary or that in any given year the patterns could be reversed. More specific possible explanations for these

differences are preferences for specific prey items among individual predator species or different physiological, physical, energetic, or time constraints imposed on each of the sympatrically occurring species.

The present study found that SSL on Lovushki Island foraged almost exclusively on Atka mackerel and NFS fed primarily on northern smoothtongue, cephalopods, and salmon. While Atka mackerel certainly are important prey items for SSL across much of their range, from the Russian Far East to the Western Gulf of Alaska, there is no evidence to suggest that they are a preferred prey item and would be selected by SSL in favor of other available prey items. Nor is there any evidence to suggest that the prey types selected by NFS, such as cephalopods or northern smoothtongue, would be avoided by SSL in favor of other available prey items, such as Atka mackerel. For example, on Raykoke Island, an SSL rookery approximately 50 km southwest of Lovushki, the most frequently occurring prey item found in scats between 2003–2008 was Atka mackerel (FO = 76%); however, the SSL at this location did not exhibit the degree of dietary specialization as SSL on Lovushki. Salmon (FO = 62%), northern smoothtongue (FO = 47%), and cephalopods (FO = 35%) were all common and important components of SSL diet on Raykoke Island (Waite and Burkanov, unpublished data), thus suggesting that allopatric SSL are as likely to select those prey items as they are Atka mackerel when available.

Another possible explanation for the pattern of resource partitioning observed is that each predator is forced into its selection of diet and foraging location based on physiological or physical limitations on foraging ability. Steller sea lions are known to

dive to depths >250 m while foraging (Merrick and Loughlin 1997, Loughlin *et al.* 1998), and although NFS are typically shallow divers, with "deep-diving" individuals averaging 50–100 m, adult female NFS are capable of making dives to depths >200 m (Gentry *et al.* 1986a, Goebel *et al.* 1991, Ponganis *et al.* 1992). During the summer, Atka mackerel are typically found at depths <200 m (Gorbunova 1962, McDermott and Lowe 1997), well within the diving range of both SSL and NFS. Almost 70% of foraging bouts performed by SSL on Lovushki Island occurred in waters <50 m, suggesting a relative abundance of Atka mackerel in shallow waters well within the average dive depth of NFS foraging on non-vertically migrating prey species (Gentry *et al.* 1986a). Although SSL tend to restrict their movements to nearshore waters, the adult females of neither species are physically or physiologically restricted with respect to foraging trip distance or duration, and thus are both capable of capitalizing on offshore aggregations of squid and northern smoothtongue. Furthermore, with their ability to dive to depths exceeding 400 m (Thomton *et al.* 2008), adult SSL could conceivably forage on squid and northern smoothtongue during the day when they are at depths beyond the diving range of NFS, providing an opportunity for a temporal partitioning of the foraging grounds. Although deep diving by both species is uncommon, most likely due to drastically increased energetic costs, none of the primary prey items consumed by Lovushki Island pinnipeds are beyond the foraging capabilities of either predator.

Though the prey selection of adult female NFS and SSL on Lovushki is not restricted by their respective foraging capabilities, the length of time each species can be away from the rookery is restricted by the different fasting capabilities of their pups. SSL

pups begin to lose lipid mass within 16 hours of the onset of a fast (Rea *et al.* 2000), thus substantially restricting the maximum foraging trip duration of female SSL with dependent young. The amount of time a female NFS with a dependent pup can remain at sea, however, is likely not nearly as limited, as the fasting capabilities of pups of similar fur seal species are considerably greater than those of SSL pups. The shorter foraging trip duration required of female SSL with dependent young restricts both the distance from the rookery that they can travel and, based on the relatively shallow nearshore bathymetry, the types of prey available for consumption. Thus, the foraging pressure by SSL in the nearshore waters of Lovushki Island is greatly increased as a result of the physiological limitations of their pups. It is this increased foraging pressure and the need to reduce inter-specific competition that likely influences NFS to travel further offshore to feed, not the physical or physiological limitations of the females or their pups. As NFS move further offshore to feed, the water depth dramatically increases and benthic prey quickly become out of reach, forcing a higher reliance on pelagic prey items, thus resulting in a significantly different diet composition.

Juvenile NFS, however, show a biologically significant dietary overlap with female SSL. Since Atka mackerel is the primary prey of juvenile NFS, with salmon, northern smoothtongue, and cephalopods comprising a substantially smaller proportion of their diet, it likely that juvenile NFS forage in habitats similar to those used by female SSL. Therefore, there is a potential for a high level of inter-specific competition between these two groups and, if the juvenile NFS population continues to increase, the possible competitive exclusion of SSL from Lovushki may result.

However, nothing specific is known regarding when and where juvenile NFS on Lovushki Island forage, other than the generalities that can be inferred from their estimated diet. It is possible that the juvenile NFS and adult SSL partition their foraging grounds differently than adult NFS and SSL. Juvenile NFS may target groups of smaller, non-breeding Atka mackerel in the water column, while the SSL feed primarily on larger, breeding Atka mackerel on the bottom, thus partitioning their foraging resources vertically as well as by prey size. This explanation is plausible given the higher proportion of walleye pollock in the juvenile NFS diet, as pollock themselves tend to feed within the water column.

Foraging by SSL takes place throughout the day, though the majority of their foraging effort is concentrated during the late afternoon and night. Juvenile NFS may take advantage of the nocturnal patterns of the SSL and concentrate their foraging efforts during the daylight hours, thus temporally partitioning the foraging grounds and reducing the numbers of competitive interactions.

Juvenile NFS are not restricted with regards to foraging trip distance or duration by dependent young, and though it is evident that they foraged in similar habitats as SSL, they may have foraged in the shallows surrounding Shiashkotan Island, 20 km to the northeast of Lovushki. This possible difference in foraging location may also explain the considerably higher levels of walleye pollock in the juvenile NFS diet, as well as the difference in the size of Atka mackerel targeted, and may be a form of spatial partitioning to reduce inter-specific competition.

Finally, in its simplest form, the competitive exclusion principle says that complete competitors cannot coexist. This purposely ambiguous wording (Hardin 1960) leaves open the interpretation of the meaning of "complete competitors." If we assume that complete competitors include those animals with similar life histories and ecological, physiological, and energetic requirements, then it is questionable whether or not adult SSL and juvenile NFS would be considered complete competitors. Though over the course of their lives, they share similar life histories, they are at different developmental stages and thus have quite different energetic needs. Breeding SSL must optimize their foraging strategy in order to maximize the amount of energy delivered to their pups while still providing for their own energetic needs. This requires strictly balancing the amount energy gained by foraging, the amount of energy spent to obtain prey, the amount of energy delivered to their pups, and the amount of time spent on each activity. Juvenile NFS, on the other hand, must only feed themselves while tending to their own social and grooming activities and, thus, do not face the same energetic and time constraints. Therefore, it is questionable whether or not juvenile NFS feel the same pressure from inter-specific competition as breeding NFS, as they have a much broader leeway with respect to time budgets, the selection of prey with lower energetic values, the relative amount of food required, and foraging location. However, it is probable that the breeding SSL feel some added pressure from the presence of an increasing juvenile NFS population, as they are restricted with respect to foraging location and thus their population growth on Lovushki may be limited by the supply of nearshore prey being reduced by juvenile NFS consumption.

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